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ANNALS
OF THE
MISSOURI BOTANICAL GARDEN

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Annals
of the
Missouri Botanical
Garden



Volume II
1915

With Twenty-seven Plates and Seventy-nine Figures

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Editorial Committee

George T. Moore

Benjamin M. Duggar

Information

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Annals

of the

Missouri Botanical Garden

Anniversary Proceedings

VOL. 2

FEBRUARY-APRIL, 1915

Nos. 1 AND 2

THE TWENTY-FIFTH ANNIVERSARY CELEBRATION

The twenty-fifth anniversary of the organization of the Board of Trustees of the Missouri Botanical Garden was celebrated at the Garden on October 15 and 16, 1914. A list of the American and foreign scientists in attendance, the complete program of the anniversary exercises, the banquet proceedings, and the papers presented at the scientific meetings will be found respectively on pages 1-3, 4-5, 6-27, and 29-401.

DELEGATES AND VISITING SCIENTISTS

- | | |
|--|---|
| MR. S. ALEXANDER
Detroit, Michigan | DR. I. W. BAILEY
Bussey Institution, Jamaica Plain,
Massachusetts |
| DR. FRANK M. ANDREWS
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tiania, Norway
- DR. WILLIAM L. WOODBURN
Northwestern University, Evanston,
Illinois
- DR. R. B. WYLIE
State University, Iowa City, Iowa

PROGRAM

Thursday, October 15

- 10:30 A. M. AUTOMOBILE RIDE THROUGH THE CITY FOR DELEGATES
AND VISITING SCIENTISTS
1:00 P. M. LUNCH AT THE GARDEN
2:00 P. M. FIRST SCIENTIFIC PROGRAM (Graduate Lecture Room)

ADDRESS OF WELCOME - - - Director George T. Moore

THE VEGETATION OF MONA ISLAND

DIRECTOR-IN-CHIEF N. L. BRITTON
New York Botanical Garden, Bronx Park, New York

THE FLORA OF NORWAY AND ITS IMMIGRATION

PROFESSOR N. WILLE
University of Christiania, Christiania, Norway

THE PHYLOGENETIC TAXONOMY OF THE FLOWERING PLANTS

PROFESSOR CHARLES E. BESSEY
University of Nebraska, Lincoln, Nebraska

THE BOTANICAL GARDEN OF OAXACA

DIRECTOR CASSIANO CONZATTI
Botanical Garden of the State of Oaxaca, Mexico
(Read by Title)

THE SCIENTIFIC SIGNIFICANCE OF THE IMPERIAL BOTANIC
GARDEN OF PETER THE GREAT, WITH SPECIAL

REFERENCE TO THE FLORA OF ASIA

DR. WLADIMIR I. LIPSKY
Jardin Impérial Botanique de Pierre le Grand, St. Petersburg, Russia
(Read by Title)

COMPARATIVE CARPOLOGY OF CRUCIFERAE WITH VESICULAR

FRUITS—SOME GENERAL BIOLOGICAL AND

SYSTEMATIC CONCLUSIONS

DIRECTOR J. BRIQUET
Jardin Botanique de la Ville Genève, Genève, Switzerland
(Read by Title)

THE ORIGIN OF MONOCOTYLEDONY

PROFESSOR JOHN M. COULTER
University of Chicago, Chicago, Illinois

THE HISTORY AND FUNCTIONS OF BOTANICAL GARDENS

ASSISTANT DIRECTOR ARTHUR W. HILL
Royal Botanic Gardens, Kew, England
(Read by Title)

8:30—11:30 P. M. RECEPTION. DIRECTOR'S RESIDENCE

PROGRAM (*Continued*)

Thursday, October 16

10:30 A. M. SPECIAL PERSONALLY CONDUCTED TRIP THROUGH THE
CONSERVATORIES AND GROUNDS OF THE GARDEN; IN-
SPECTION OF LABORATORY, LIBRARY, AND HERBARIUM.

12:30 P. M. LUNCH AT THE GARDEN

1:30 P. M. SECOND SCIENTIFIC PROGRAM (Graduate Lecture Room)

RECENT INVESTIGATIONS ON THE PROTOPLASM OF PLANT CELLS
AND ITS COLLOIDAL PROPERTIES

PROFESSOR FREDERICK CZAPEK

Physiologisches Institut der K. K. Deutschen Universität, Prag, Austria

(Read by Title)

EXPERIMENTAL MODIFICATION OF THE GERM-PLASM

DIRECTOR D. T. MACDOUGAL

*Department of Botanical Research, Carnegie Institution of Washington,
Tucson, Arizona*

HORMONE IM PFLANZENREICH

DIRECTOR HANS FITTING

Botanische Anstalten der Universität Bonn, Bonn, Germany

(Read by Title)

THE RELATIONS OF SCIENTIFIC BOTANY TO PHYTOPATHOLOGY

GEHEIMER REGIERUNGSRAT DR. O. APPEL

*Kaiserlichen Biologischen Anstalt für Land- und Forstwirtschaft,
Berlin-Dahlem, Germany*

THE LAW OF TEMPERATURE CONNECTED WITH THE DISTRIBUTION
OF MARINE ALGAE

PROFESSOR WILLIAM A. SETCHELL

University of California, Berkeley, California

UEBER FORMBILDUNG UND RHYTHMIK DER PFLANZEN

DIRECTOR GEORG KLEBS

Botanisches Institut Universität Heidelberg, Heidelberg, Germany

(Read by Title)

PHYTOPATHOLOGY IN THE TROPICS

DIRECTOR JOHANNA WESTERDIJK

Phytopathological Laboratory, Amsterdam, Holland

PHYLOGENY AND RELATIONSHIPS IN THE ASCOMYCETES

PROFESSOR GEORGE F. ATKINSON

Cornell University, Ithaca, New York

THE ORGANIZATION OF A MUSHROOM

PROFESSOR A. H. REGINALD BULLER

University of Manitoba, Winnipeg, Canada

(Read by Title)

A CONSPECTUS OF BACTERIAL DISEASES IN PLANTS

DR. ERWIN F. SMITH

*Bureau of Plant Industry, U. S. Department of Agriculture,
Washington, D. C.*

7:30 P. M. TRUSTEES' BANQUET. LIEDERKRANZ CLUB.

BANQUET

MR. EDWARDS WHITAKER

Toastmaster

Ladies and Gentlemen: This being an epoch in the history of the Missouri Botanical Garden, it was thought that a short biography of its founder and benefactor would be interesting.

Henry Shaw was born in Sheffield, England, July 24, 1800. He received his primary education at Thorne, a village a few miles distant from his birthplace, and at this early age developed a fondness for flowers and plants. Completing his course at Thorne, he continued his education at Mill Hall, twenty miles distant from London, where he was a student for six years.

In 1817 he entered the service of his father, who was a manufacturer and dealer in metal wares, such as andirons, grates, etc.

In 1818 his father sailed from England with his family for America, landing in Canada. We are without reliable information as to the exact place in which he located. The same year, probably in the late fall, he sent his son to the city of New Orleans to familiarize himself with the planting and growing of cotton. The climate of New Orleans did not suit him and the business was not to his liking, and his stay in Louisiana was short. He decided to seek his fortunes elsewhere, and so took passage on the "Maid of Orleans," and landed at St. Louis, May 3, 1819.

With the assistance of his uncle, James Hoole of Sheffield, he started a cutlery and hardware business in a room on the second floor of a building in the business district, which served as warehouse, show-room, office, and dwelling, doing his own cooking and housework, as he was without, and never was blessed with, a better half.

His business was successful and uniformly profitable, and, at the age of 39, he had amassed a fortune, as he thought, large enough for any one and sufficient to gratify his taste for botany and the sciences.

He retired from business in 1840, and took a trip abroad, the first since leaving his native shore. This trip was evidently of short duration, as in 1842 he arranged his affairs and sailed a second time for the Old World, remaining three years, traveling extensively and making the acquaintance of botanists and scientists.

Holding the English idea that a gentleman of fortune and leisure should maintain a town house and country home, he commenced the erection of his country home on the Garden grounds in 1848, completing it in 1849, and in 1851 built his town house at the corner of Seventh and Locust Streets, the site now occupied by the Mercantile Club.

His last trip abroad was in 1851, and in 1858 he commissioned Dr. George Engleman of this city, a noted botanist then traveling in Europe, to procure material and information that he thought would be of service to a botanical garden; and at the suggestion of Sir William J. Hooker, then Director of Kew Gardens, began to prepare a laboratory and erected a museum building, and this was the commencement of Shaw's, now the Missouri Botanical, Garden.

While constructing the garden along the lines suggested by Sir William J. Hooker, he commenced the improvement of a tract of land immediately south of the Garden, now known as Tower Grove Park. In 1857 he had an act of the legislature passed authorizing the city to receive, under certain conditions, as a donation this tract for a park. Among them was that the park was to be managed and controlled by a board of park commissioners of his appointment; secondly, that appropriations were to be made sufficient to complete it in accordance with the plans already adopted; and the third condition, that an annual appropriation sufficient for its maintenance should be made; and in 1868 he deeded the property to the City.

Having in mind the conveying to Trustees of his estate to be administered by them for the benefit of the Garden, and a question having arisen whether such a trust was legal and could be administered in this state, he had an act of the legislature passed declaring his intentions, and authorizing him to

transfer his property to trustees and further declaring it lawful. Shortly afterwards, the Supreme Court of the state decided in the case of Chambers vs. The Mullanphy Relief Fund Bequest, that such trusts were legal and could be administered in this state, thereby removing the doubt entertained by some of the legal profession.

In 1866 Mr. Shaw secured the services of Mr. James Gurney from the Royal Botanical Garden in Regents Park, London, who was Head Gardener during Mr. Shaw's lifetime and for several years afterward, and is now Head Gardener Emeritus, and also Superintendent of Tower Grove Park.

There is no record of Mr. Shaw ever having had a public opening of the Garden, and a committee of trustees appointed to investigate and report on the date the Garden was established, decided that the Missouri Botanical Garden began its existence in 1889, upon the organization of the trust declared by Mr. Shaw's will.

Mr. Shaw executed his will January 26, 1885, devising his estate, with the exception of a few minor bequests, to a board of trustees of seventeen, the original members of which were designated in the will, and the board thus constituted, exclusive of certain *ex-officio* members, was to be self-perpetuating. The five trustees by virtue of the offices they hold were the Mayor of the City of St. Louis, the Chancellor of Washington University, the Episcopal Bishop of the Diocese, the President of the Board of Public Schools, and the President of the St. Louis Academy of Science. There were two honorary trustees appointed, Professor Asa Gray of Harvard University, and Professor Spencer F. Baird of the Smithsonian Institution.

Before the death of Mr. Shaw, on August 25, 1889, and the probating of his will, on September 17, both of the honorary trustees had passed away as well as two of the active members of the Board.

The remaining trustees met October 14, 1889, at Mr. Shaw's late residence, Seventh and Locust Streets, and effected an organization of the Board, electing Mr. Rufus J. Lackland President, Mr. Henry Hitchcock Vice-President, Mr. A. D.

Cunningham, Secretary and Treasurer, and appointing Professor William Trelease Director.

Immediately thereafter, by-laws were adopted and committees appointed so that the estate could be efficiently managed. There were four committees—the Garden Committee, the Auditing Committee, the Lands Committee, and the Ways and Means Committee—the President of the Board being *ex-officio* member of all committees. All actions of the committees require the approval of the Board before becoming operative.

There have been three Presidents, three Vice-Presidents, one Secretary and Treasurer, and two Directors of the Garden since the organization of the Board. Of the original trustees named in the will but one survives, Mr. William H. H. Pettus, whose feeble health prevents his being with us this evening. There are but two salaried officers connected with the estate, the Secretary and Treasurer, and the Director, the trustees serving without compensation.

And I wish here to correct an impression prevailing among many that this estate is exempt from taxation. That is erroneous. With the exception of the Garden grounds proper, the estate pays taxes the same as any citizen, and I may add that this item consumes about one-fourth of the gross income, the remainder being used for the maintenance of the Garden and other objects of the trust.

Mr. Shaw was a man of independent thought and action, and while devising his estate to trustees, he at the same time appointed the public administrator of the City of St. Louis the executor of his will.

Among provisions of the will was an annual appropriation for a flower sermon to be preached at such church and by such minister as the Bishop of the Diocese may select; an annual banquet for florists and gardeners in and about St. Louis, at which the Director of the Garden was to preside; a banquet for the trustees and the guests they may invite—literary and scientific men and friends and patrons of the natural sciences.

Another provision of the will was that his residence at Seventh and Locust Streets was to be taken down and rebuilt

upon the Garden grounds. It also provided that the Garden should be open to the public every day in the week, excluding holidays and Sundays with the exception of the first Sunday of June and September in each year, when the Garden should be open from 2:00 p. m. to sundown. This latter provision was literally carried out until the spring of 1912, when the Board thought the best interests of the Garden would be promoted by adding additional Sundays, and, having legal advice that there was no objection to their so doing, it was opened from April 1 to December 1, from 2:00 o'clock until sundown. This action proved to have been wise, as the attendance at the Garden increased threefold.

Such, briefly, ladies and gentlemen, were the objects and the accomplishments in the life of Henry Shaw, a man of whom any City, State or Nation might well be proud, and I request that this assemblage rise and drink with me, in silence, to the memory of Henry Shaw.

[This toast was then drunk by those assembled.]

The Toastmaster then presented as follows the apologies of the Hon. Henry W. Kiel, Mayor of the City of St. Louis, who had been expected to respond to a toast:

Mr. Shaw in his wisdom appointed as one of the Trustees the highest official of the City of St. Louis. He was with us a short time this evening and was compelled to leave, owing to a previous engagement that he thought it would be impossible to break, and I have promised him to make his apologies for not remaining.

In introducing the next speaker of the evening, Dr. Johanna Westerdijk, Director of the Phytopathological Laboratory, Amsterdam, Holland, the Toastmaster spoke as follows:

We are complimented by the presence this evening of a lady from a foreign shore, whose achievements have given her a high position in the botanical world. It is my privilege to introduce Dr. Johanna Westerdijk, of Amsterdam.

DR. JOHANNA WESTERDIJK

Mr. Chairman, Ladies and Gentlemen: This is a delightful day, but I am sorry that not our great Holland botanist is in

our midst. He would be so much more able to express his feelings for America and for the Missouri Botanical Garden, which I know he loves so well. But since he is not here, I think it is a great honor for me to express my feelings, and I know that these feelings are the feelings of all the Dutch botanists, who all love botanical gardens, from the day of Boerhaave up to recent times.

Mr. Chairman and Trustees, and Mr. Director Moore of the Botanical Garden, I thank you in the name of Holland for the delightful day, for the splendid reception I have had here; and if I may express myself in a bit of your American slang at a most solemn banquet, I thank you for the most jolly time I have had in this most delightful bunch of interesting American botanists.

Geheimer Regierungsrat Dr. O. Appel, of the Kaiserlichen Biologischen Anstalt, Berlin-Dahlem, Germany, was next called upon by the Toastmaster in the following words:

We have been favored by the presence of a number of foreigners, among them a neighbor of Dr. Westerdijk, and I trust that, being in the Liederkranz Club, he will feel sufficiently at home to give us his impressions of our country, through which he has travelled extensively. I take pleasure in introducing Dr. O. Appel, of Berlin.

DR. O. APPEL

Ladies and Gentlemen: If I should speak to you of my botanical or phytopathological work, I could use your language; but to express my feelings I must use my mother tongue, the German language!

Sie haben zu dem Tage, den Sie heute festlich begehen, auch eine Anzahl europäischer Fachgenossen eingeladen und die Beteiligung von einer groszen Anzahl erwartet. Die Gründe, die die meisten Ihrer europäischen Gäste am Erscheinen verhindert haben, sind Ihnen bekannt und werden wohl von Ihnen allen bedauert.

Dasz eine grosze Anzahl hervorragender Vertreter des Auslandes hier erwartet wurde, hat seine Berechtigung, denn in den Jahren seines Bestehens hat der Botanische Garten von

St. Louis sich würdig in die Reihe der grösseren derartigen Institute eingegliedert, und trotz der grossen Entfernung hat schon mancher europäische Botaniker diese Stätte der Wissenschaft ausgesucht und die Kunde von seiner raschen Entwicklung in ferne Länder getragen.

Aber nicht nur durch den Beweis sind die Bande zwischen unseren deutschen Botanikern und den am Shaw's Garden arbeitenden Fachgenossen geknüpft worden, auch durch mannigfachen Austausch von Material und Gedanken haben sich viele Beziehungen ergeben, die heute eigentlich ihren Ausdruck durch das Erscheinen einiger unserer bedeutendsten Fachgenossen, Klebs und Fitting, ihren Ausdruck haben finden sollen.

Da dies nun nicht sein konnte und äussere Umstände mir als dem einzigen deutschen Botaniker die Teilnahme an Ihrer Feier vergönnt haben, so möchte ich nicht versäumen, Ihnen im Namen der deutschen Botaniker die besten Wünsche auszusprechen.

Fünfundzwanzig Jahre erscheinen als eine kurze Spanne Zeit und doch haben Sie ein Recht den Abschluss dieser fünfundzwanzig Jahre zu feiern. Dieser erste Zeitabschnitt ist einer der wichtigsten, vielleicht überhaupt der wichtigste, denn in ihm sind die Grundlagen für die ganze Zukunft des Gartens geschaffen worden. Was in diesen Jahren geschaffen worden ist, das haben Sie alle gesehen. Noch erkennt man da und dort die kleinen und einfachen Verhältnisse, unter denen die Arbeit begonnen worden ist, aber daneben und sie überragend hat schon die neue Zeit dem Garten und seinen Gebäuden ihr Gepräge aufgedrückt. Überall sieht man, mit welcher Planmässigkeit und Groszzügigkeit die Entwicklung gefördert worden ist und wie sowohl der wissenschaftlichen Arbeit, wie der Nutzbarmachung für die grosse Allgemeinheit in jeder Weise Rechnung getragen wird.

Aber auch denen, die nicht in der Lage sind, die Schätze des Gartens, der Laboratorien direkt zu benutzen, haben Sie eine Quelle der Belehrung und Anregung gegeben durch die Herausgabe der beiden periodischen Schriften 'Annals of the Missouri Botanical Garden' und 'Missouri Botanical Garden

Bulletin,' von denen die erste für die Gesamtheit der botanischen Welt bestimmt ist, während die letztere sich an alle die in Ihrer eigenen Heimat wendet, die für die Botanik als *scientia amabilis* Sinn und Verständnis haben.

So gehört denn keine grosze Prophetengabe dazu, dem Shaw's Garden eine weitere gedeihliche Entwicklung vorherzusagen.

Dasz aber auch die deutschen Botaniker immer da, wo sie können, und wo ihre Mitwirkung erwünscht ist, gerne mit Ihnen Hand in Hand arbeiten werden, dafür bringt Ihnen die Art der deutschen Wissenschaft, die stets die Förderung jeglicher Forschung zum allgemeinen Besten im Auge gehabt hat und auch in der Zukunft als höchstes Ziel im Auge behalten wird, den Beweis.

Meine Wünsche aber erlauben Sie mir zusammenzufassen in den Ruf:

Hortus botanicus Shawensis vivat, crescat, floreat!

(A translation of Dr. Appel's address follows.)

For this day which you are celebrating, you had invited also a number of European colleagues and expected that of these a large proportion would participate in the exercises. The causes which have prevented most of your European guests from being present are known to all of you and doubtless are regretted by you all.

The expectation of a larger number of foreign representatives is justified, for during the years of its existence, the Botanical Garden of St. Louis has deservedly taken its place in the ranks of the larger institutions of its kind, and, despite the great distance, many a European botanist has already sought out this scientific center and carried the message of its rapid development to distant lands.

But the ties that exist between our German botanists and their colleagues working at Shaw's Garden have been established not alone by such visits, but also by the abundant exchange of material and ideas, in which relationships have developed which to-day were to have found expression through

the appearance and participation of two of our most noteworthy colleagues, Klebs and Fitting.

But since this could not be, and circumstances have graciously willed it that I should be the only German botanist to participate in your celebration, I wish to express to you on behalf of the German botanists our best wishes.

Twenty-five years appear as a short interval of time and yet you have a right to celebrate the completion of these twenty-five years. This first period is one of the most important, if not the most important, for in it have been established the foundations for the entire future of the Garden. You have all seen what has been created in these years. One still recognizes here and there the simple conditions under which the work was started, but these are eclipsed by the imprint which later years have left on the Garden and its buildings. One sees everywhere with what ability and foresight the development of the Garden has been promoted and every provision made for the scientific work and the increased usefulness of the Garden to the public.

But you have also provided a source of information and stimulation to those who are not in a position to directly make use of the resources of the Garden by the publication of the two periodicals, 'Annals of the Missouri Botanical Garden' and 'Missouri Botanical Garden Bulletin,' of which the former is intended for the entire botanical world, whereas the latter goes to those in your home who have an interest in, and an understanding for, botany as a *scientia amabilis*.

It does not, therefore, require a great gift of prophecy to predict for Shaw's Garden a further deserving development.

Wherever German botanists can help and wherever their coöperation is desired, they will always gladly work hand in hand with you, proof of which is furnished by the very character of German science, which has always sought to further each and every investigation for the greatest general good, an ideal which will not be lost sight of in the future.

My wishes you will permit me to express thus:

Hortus botanicus Shawensis vivat, crescat, floreat!

The Toastmaster next called upon Professor N. Wille, of the University of Christiania, Christiania, Norway, as follows:

We have also a friend and botanist from Norway, who, I understand, had a rather peculiar experience in this country. He told me that he had for forty-eight hours or more lost his better half by having the tickets and she starting without any Pullman accommodations. I know he can talk to us interestingly, and we will be glad to hear from Professor N. Wille, of Christiania.

PROFESSOR N. WILLE

The Members of the Board of Trustees, Fellow Scientists, Ladies and Gentlemen: I am deeply grateful to the members of the Board of Trustees of the Missouri Botanical Garden for the kind invitation to participate in this celebration. Had it not been for this I should perhaps never have known America. In the short time that I have been here I have learned much, and I only regret that it is not possible for me to remain in your country longer. When I see the splendid botanical equipment of the Missouri Botanical Garden, I can only lament that it has not been possible for me to prosecute my work under such unusually favorable circumstances. My best wishes for the continued scientific development of the Missouri Botanical Garden.

In introducing Captain Henry King, the Toastmaster spoke as follows:

We have now reached one of the very many interesting subjects of the evening, namely the press. Who is there among us who has not, at some time and some place, received flattering notices at its hand, while again, hard knocks, administered without warning and at the most unexpected moment. If I may be permitted to make a suggestion to the speaker who is to follow me, it is that he go easy with us scientists and delvers in the soil, and in the language of a son of Erin's Isle, "If you can't go easy, go as easy as you can." It is my privilege to introduce Captain Henry King, Editor of the 'St. Louis Globe-Democrat.'

CAPTAIN HENRY KING

It is the paramount duty of the newspaper editor to tell the truth. I do not mean literally and completely, but approxi-

mately and within the rule of reason and the zone of safety. Less is expected of other people, apparently, or the editor would not so often find it so hard to get the truth when he wants to print it. Take, for example, the tremendous and deplorable situation now presented in Europe. With all our anxiety and all our facilities, we can not be certain how much or how little of the wild and whirling daily reports from there—news from hell, so to speak—is dependable. We have not yet even found out definitely what it is all about, and why hundreds of thousands of industrious and inoffensive citizens have been taken from their homes and affairs, and sent forth with all kinds of murderous weapons to slay one another as fast as possible. The most that we can be sure of is that a war of unparalleled dimensions and appalling severity is raging, and that about the only really good thing in it is that white messenger of pity and succor, the Red Cross nurse. And yet I am assured by a leading St. Louisan just returned from the seat of war that the reports in the St. Louis papers are more rational, consistent and enlightening, after all, than those in the papers of any of the cities on the other side of the Atlantic. This man's word is good and his judgment accurate. You all know him. I refer to the Hon. Charles Nagel.

The lesson of Mr. Nagel's gratifying statement is a timely and an important one. It goes to show that in a case of worldwide interest and illimitable consequences, where the truth veritably lies at the bottom of a well, the St. Louis press gets nearer to it by care and candor, by unprejudiced analysis and fair-minded discrimination, than the press of Europe. This example is an extreme one, perhaps, but I feel safe in saying that it is characteristic and relatively prevalent in all cases. I am here, as you have been advised, to talk about the press, or at least to use it as a text. You do not expect me, I am sure, to stand here on this festive and botanical occasion and confess the sins of my esteemed contemporaries, or to acknowledge my own, for that matter. So, if you please, I am going to sidestep the sins, for the present, and declare from personal knowledge and daily comparison that St. Louis has ample reason to be proud of her newspapers. They are not perfect, to be sure,

which is only saying that human life is not perfect, for they are made out of life as life is lived in this goodly city and elsewhere from day to day. They tell you the current history of the community, of the country, of the universe, and they tell it as correctly as the limitations of human nature permit. They have defects of temperament, faults of accident and misinformation, I frankly admit. If they had not these delinquencies, mingled with their excellences, as has the life out of which they are made, they would soon become too good for this world and their home would be in heaven, and you would not have any use for them here on this rolling and imperfect planet. They make mistakes, yes—just as you do, and all men (and some women) do, just as the busy life out of which they are made is in great measure a matter of mistakes, which constitute what we call experience, and experience is only another name for news.

Bear with me, I beg you, if I seem to be too ardent in this topic of the St. Louis press. But I am putting aside, for this occasion, the proverbial modesty of my profession, with a view to telling you the naked truth as if I were under oath. And let me remind you, while I think of it, that the only monument in the world to "The Naked Truth" stands only a short distance from where we are assembled, and its purpose is to typify and commemorate the lives and services of three great St. Louis newspaper editors, Schurz, Preetorius and Daenzer. I am talking to you of the successors of those men, whom I know like a book—my neighbors, my friends, my fellow-workers—the men who direct and adorn and give tone and influence to the St. Louis press. I know them to be tireless in their pursuit of facts, in their zeal for the public welfare, in their ambition to promote the growth and progress of this admirable city. It is sometimes said in criticism of them that they are governed mainly by commercial considerations, and one of the pestiferous sort of professional reformers has lately sent forth a book in which he goes so far as to charge that their policies are absolutely dictated by their big advertisers. Well, if it wasn't for the big advertisers, you would hardly be able to get the modern wonder and recognized necessity of a daily newspaper

for the absurd price of a penny a copy, the cheapest of all known commodities of general use; and I often think that the advertisements constitute the most interesting and serviceable part of the paper. That is not the only reason why we print so many of them, I am bound to admit, but it certainly tends to ameliorate the condition and to make the habit almost innocent. As for the advertiser as a dictator of editorial policy, we do not find him very insistent or obstreperous. In a lifetime of experience, I have never yet known an advertiser to solicit any selfish advantage or assert any right of arbitrary interference on account of his patronage; but it is a common thing to have them come forward in earnest and practical support of projects for the common good. We owe it largely to the advertisers, the business men, that we have the Veiled Prophet with us every year; that we had an incomparable World's Fair; that we produced the unequaled Pageant and Masque; and I don't believe they will permit the reproach of failure to overtake the Symphony Orchestra. And I'm going to include the Free Bridge in this assurance, though just now I do not see any practicable way to connect with it.

This brings me to the point of chief interest, to the Missouri Botanical Garden, with its immense display of floral splendor, its infinite sources of delight and instruction, of admonition and of consolation. I wish I could botanize about it in the thorough and skillful manner of our distinguished scientific visitors. But alas, I have to make the bashful admission that I probably know less about botany as a science than any other person on your program to-night—unless it may be your Toastmaster. The fact is, I have had less to do with flowers than with quadrupeds, such as the Donkey, the Bull Moose, and the Elephant—God bless him—begging the pardon of those of you who don't happen to like him as well as others of us do. But I am tolerably familiar with the part which flowers have played in the affairs of the world. I know how all literature is pervaded by their fragrance and their symbolism. I am not unmindful of their cherished associations in the lives of all classes, from the cradle to the grave. I know how, in many instances, when wisdom reaches its limit and language fails,

they have the gift of talking to us and for us, in a form of expression which we can grasp only with our feelings and emotions, and which our hearts rather than our heads must interpret and utilize.

But I must not deviate too far from the relation of the editor to floriculture, which is similar to that of the boy in Mr. Lincoln's story who, being asked if he liked gingerbread, replied, you remember, "I reckon I like gingerbread better than any boy in this town, and get less of it." So it is mainly with the editor and the bouquets. He is more apt, as a rule, to have stale vegetables thrown at him, figuratively speaking, and to be condemned to wait for his flowers until he reaches that point in his career where he no longer has use for anything else. But, happily, the editor is nothing if not a philosopher. The discipline of his profession teaches him patience and tolerance and sweet reasonableness. In the nature of things, he gives more attention to other people's affairs than to his own—so much so, indeed, that now and then he is accused of being over-zealous, not to say over-inquisitive, in that respect. If a bouquet comes his way it surprises and confuses him, since it contradicts his personal experience that if virtue be not its own reward, then it usually remains unrewarded. Nevertheless, he goes on boosting instead of knocking, because it is his mission to spread the gospel of good cheer and make more room in the sun for those who inhabit the earth. He welcomes particularly an occasion like this, where he can help to celebrate the choice taste, the fine civic spirit, the munificent public benefaction of a man like Henry Shaw. And his pleasure is doubled when to such an opportunity is added the chance to compliment the Missouri Botanical Garden upon having for President of its Board of Trustees a man with the many excellent qualities of Edwards Whitaker. Science is the basis of the great enterprise which Mr. Shaw founded, of course, but science needs trained business sense to invest its service with the highest practical usefulness. Mr. Whitaker has shown in a marked degree his realization of the possibilities of his position, and the steps by which the benefits of Shaw's Garden, as we familiarly call it, can be materially multiplied. I feel

authorized to say that in this important work he will have the hearty coöperation of the St. Louis press; and I am sure that he will in turn see to it that the editors get all the floral tributes that are due to them, at least when the time arrives for them to confront the ultimate River of Separation, and each of them shall need something of that sort to waft aloft in his behalf the beautiful message of Tennyson—

“For though from out our bourne of time and place,
The flood may bear me far,
I hope to see my Pilot face to face
When I have crossed the bar.”

In the following words the Toastmaster called upon the next speaker of the evening, Dr. William G. Farlow:

We have with us this evening a guest who, I can truthfully say, is loved by every botanist in America, and I can also assert without fear of contradiction that he is recognized as their dean. I am proud to introduce Dr. William G. Farlow, of Harvard University.

DR. WILLIAM G. FARLOW

Mr. President and Ladies and Gentlemen: As I look upon this company and see how many there are here, all of whom are interested in the St. Louis Botanical Garden, I can't help asking myself the question: “Why are they interested in the Garden?” Some have one reason; some have another. Some like it for the flowers that are shown there; some like it for the scientific work done there. But whatever their reasons may be, I would like to take advantage of this occasion to say a few words about what seems to me to be the true object and aim of botanical gardens.

Let us go back to history. The first garden on record, I believe, was the Garden of Eden. That garden unfortunately was obliged to be closed to the general public only a short time after it was opened. But we learn some lessons even from the Garden of Eden. In the first place, do not mix zoölogy and botany. The Garden of Eden was not purely a botanical garden. You know what the snake did and will always do in botanical gardens. There is another curious thing about the

Garden of Eden. It is the only garden I ever heard of from which people were excluded because they had just begun to learn something, and it seems to be exceedingly cruel that they should have been turned out into a cold world merely because they knew something.

But it is a long step from the Garden of Eden, and history is a little more accurate in recent times than it was then. The traditional botanical garden, the one which has existed for centuries in Europe and to a less extent in this country, was a place where the seeds of a great many plants were sown; some came up and some did not, but they were all labelled. Now many plants are annual but labels are perennial and the unfortunate result in many of the older gardens was that there was a luxuriance of labels and a comparative poverty of plants corresponding to the labels.

The ideal garden is nature. We can never equal nature in anything like proximate perfection. Go up in the mountains or go out into the woods. You see nature where it has existed for ages, the result of centuries of work. What we see is not what has been planted a few years before. It is the result of the conflict of ages going on between natural forces, and what we see is the final result, such as can not be obtained by man. We find plants which grow where they naturally grow; we see moss where moss should grow; we see trees where trees should be. In a botanical garden of the present day, such as the Missouri Botanical Garden, we should imitate nature as far as is possible in a limited space and offer to the general public and the special students of botany an epitome of the vegetation of the world.

Those of our botanists who visited the Garden yesterday and to-day saw a superb display of cosmos. I don't know that St. Louis people fully appreciate what a fine exhibition of flowering plants we have seen here, but the cosmos are perfectly magnificent and you have reason to be proud of them. I hope your spring flowers are equally splendid, and there is no reason why in the summer you can't have groups of equally fine character. The old-fashioned botanical gardens had no beauty whatever. They were simply artificial and repulsive,

but at present a botanical garden must in the first place be beautiful. Although beauty is not the end of everything, we begin with beauty and end with science both practical and theoretical. Besides the flower beds and hothouses the casual visitor notices certain buildings of considerable size scattered here and there. What they are for is not perhaps known to many of those attracted by the floral display. Without these buildings and their contents and the experts in charge of them there could be no floral display of any real importance. Although they add little to the beauty of the Garden, in these buildings is done the work which gives to the Garden its scientific value and entitles it to recognition throughout the botanical world. The very valuable library and herbarium are, in a sense, the soul of the Garden, since from them is obtained a knowledge of the plants cultivated, and they are a necessity to those carrying on research in the laboratories.

At this late hour I cannot enter into details. It should be said, however, that for the library and herbarium, fire-proof buildings, always expensive, are necessary since if destroyed they could not be replaced by insurance. The laboratories for research are in a somewhat different position. The value of research in vegetable physiology and pathology and other subjects other than systematic botany, which is, of course, carried on in the herbarium, cannot be overestimated. Convenient and well-equipped laboratories are a necessity in a modern garden. They do not, however, require expensive fire-proof buildings. The outfit of the laboratories should be up to date, but new and improved instruments are invented from year to year and an occasional conflagration is not to be dreaded since the insurance on the older instruments can be used for purchasing better new ones. Furthermore, the trend of original research is constantly changing and, in trying to adapt themselves to the current demands of the scientific public, the nature of the work done in research laboratories and in consequence their equipment vary from time to time.

As I look at my audience, I am reminded of something I saw in the train coming to St. Louis the other day. I picked up what I believe was the last number of 'Life,' and glanced at

a cartoon, a crowd of persons seemingly very much pleased, and wishing to know why they were hilarious, I saw that the title was the "Millenium Celebration in Honor of the Abolishment of After Dinner Speeches." Your faces remind me somewhat of those of the crowd I saw in 'Life,' and I now close, fearing that you may be hoping that the millenium will arrive before we have another twenty-five year dinner, when I shall not be with you.

The Toastmaster next called upon the Hon. Charles Nagel, of St. Louis, in the following words:

Our city has had a number of her sons, and adopted sons, called to occupy positions of responsibility at the National Capital, one of whom, after four years' service in the Cabinet, has returned to the city of his adoption; and I am proud to introduce the Hon. Charles Nagel, ex-Secretary of Commerce and Labor.

HON. CHARLES NAGEL

Mr. Toastmaster, Ladies and Gentlemen: It appears to me that the last speaker was both wise and unkind in referring to the illustration from 'Life' at the close of his speech. I can assure him that my embarrassment was sufficient without that reference.

In endeavoring to account for my presence in a family of botanists, I have been compelled to go pretty far back in my life and to recall an incident when an aged grandmother, whom I never knew, sent me what Dr. Appel will pardon me for calling a "Botanisirbuechse," to encourage me in the collection of plants. It was only a trifle at the time, and yet I imagine I share the experience of most people in tracing my interest in nature to that early incident in my life. I would say that my love of nature is such that I would rather have my child love the virility and strength of an oak leaf than all the bouquets and flowers that can be gathered.

I believe that real love for the strength of nature is what we need, and not the pampering influences of the selected flower. I believe in the forests of New Hampshire that my friend, Dr. Farlow, loves; and I can see him now searching

for his specimens there, but never unmindful of the grandeur of all nature to which his specimen furnishes only a clue.

But studying of the plant means more than that. It means the reason of nature. I have sometimes thought that if we knew more of the reason for the decline of one plant and the triumph of another, we would have a better understanding of the meaning of the inevitable and unavoidable conflicts that are now tearing the world apart; and we Americans, if we knew more of the generating influence of the one and the survival of the other, would appreciate that it takes conflict and danger to make strong men and women.

I do not want to go too far, but while a park need not be a botanical garden, no park can succeed unless it has applied to it the science and the work of the school of botany. We can not have the city beautiful, with all our preaching, until we understand the true meaning of a school of botany and of our botanical gardens. If any one doubts it, let him look abroad. He who has seen the beautiful forests about Paris, the splendid forests about Berlin, the wonderful forests about the Hague, will say to himself, "Yes, this is nature, profound and beautiful"; but it is not an accident. It is the result of nature's force guided by experience and science.

That is what we need—politics, government, must take into counsel the man of wisdom and experience to produce those wonderful results which so far we cannot imitate. There is more than that. Abroad, not only the government utilizes the information which these men and women of science have to give, but every man and woman throughout the land consciously or unconsciously is influenced by the same teaching. Wherever you look and whatever you see demonstrates to you the result of that kind of work. It means not only the flowers and the plants, but it evidences the happiness of family life. Every field shows it; every home and every garden patch shows it. That is the lesson we have to take unto ourselves in this, our new country. That is what we have to do if, as a people, we are to succeed; and it is for this reason that we welcome the greetings of the distinguished guests who have joined us to-night.

True, all the countries are not represented; but we have the right to say to ourselves that science and civilization stand above all the conflicts of the day. Ultimately, the very nations who are now engaged in this conflict will again have to unite their hands to bear the standard of civilization jointly upon the Continent; and we have a right to say to-night that while only a few countries are represented, from the standpoint of science and civilization broadly speaking, the few representatives are here to speak to us for all the civilized nations of the world.

The last speaker of the evening, Dr. George T. Moore, was called upon by the Toastmaster as follows:

Mr. Shaw's will requires the Board to appoint a Director of the Garden, who is to reside upon the Garden grounds. He is virtually the executive of the board and the Garden Committee so far as Garden matters pertain, and he might be compared to the man behind the gun, as much of the success of the Garden depends upon him. The Director is known to so many of you, an introduction seems hardly necessary; but for form's sake I take pleasure in introducing Dr. George T. Moore, Director of the Missouri Botanical Garden.

DR. GEORGE T. MOORE

It was my pleasant task on yesterday to welcome those who honored us with their presence at the first formal exercises celebrating the passing of a quarter century in the life of the Missouri Botanical Garden. To-night has been delegated to me the duty of closing what at least for the Garden has been a most memorable festival, one which long will remain that delight which, joined with memory and hope, constitutes a perfect occasion.

An after-dinner speech is sometimes regarded as a sort of verbal culture medium for the propagation of words, and it is remarkable with what rapidity those who confine their efforts to media containing no solidifying substance can cloud an otherwise clear situation. With the example set me to-night, it behooves me to speak directly to the point and not spoil an evening which thus far has been faultless.

That the Missouri Botanical Garden was fortunate in its founder, I have tried to indicate early on this anniversary occasion, and it is not necessary, even if it were possible, for me to add anything to the appreciative words which have been spoken at this table.

I do feel, however, that perhaps not enough emphasis has been placed upon the fact that it is the organization of the Board of Trustees which furnishes the real reason for this anniversary, and that in honoring Mr. Shaw and in praising the courage and skill which he displayed, we are apt to forget the prolonged efforts of those men who have unselfishly given of their time and thought to make the dream of Henry Shaw come true.

You botanists present know that he who would keep up his scientific fire must also have the means of keeping up his material woodpile. Certainly no place in this country has a trust been so closely and so successfully administered as by that body of men who, from the very first, have labored without remuneration or recognition from those they served, the Board of Trustees of the Missouri Botanical Garden!

Every citizen of St. Louis, every visitor to the Garden, every botanist or individual who may have been assisted by the facilities of the Garden, library or collections, has reason to echo the words of George Washington, which, slightly altered, are just as applicable to the Board of Trustees of the Missouri Botanical Garden throughout its existence, as they were to Benjamin Franklin:

"If to be venerated for wisdom, if to be admired for talents, if to be esteemed for service, if to be loved for devotion, can gratify the human mind, they must have had and have the pleasing consolation that they had not and will not have lived in vain."

In the long run, which is a sort of mathematical name for Providence, such services have their reward, but every twenty-five years, I think the Board of Trustees as a body—for the individuals wouldn't permit such a thing—should at least be entitled to a public statement of the facts.

We are grateful to all who, through their active participation or by their presence at the sacrifice of valuable time and by long journeyings, have contributed to the success of this

occasion. Especially do we owe thanks to those who by presenting such splendid papers have made the programs such as will be difficult to surpass in the future.

The celebration of an anniversary is a ground of congratulation or regret according as it marks the progress or decline of the event it commemorates. My only hope at this time is that on the next anniversary occasion of the Missouri Botanical Garden the advances made along the lines of the various activities in which the Garden is interested, may be far beyond those of the present, and that the celebration will exceed the twenty-fifth as many times as the Garden is years older.

The Toastmaster concluded the program of the evening with the following remarks:

The hour is growing late. A few words before parting. On behalf of the Board of Trustees of the Missouri Botanical Garden, I wish to thank one and all for their presence here this evening, especially those who have journeyed far to be with us, and to express the hope that we may enjoy this pleasure many years to come. Good night!

ADDRESS OF WELCOME

GEORGE T. MOORE

Director of the Missouri Botanical Garden

It becomes my pleasant duty at the beginning of the program celebrating the twenty-fifth anniversary of the organization of the Missouri Botanical Garden to formally do what I am sure has already been done over and over again by each member of the staff—welcome most heartily those guests who have done us the honor of coming to share with us the simple, yet I hope adequate, ceremonies which have been arranged for this occasion. At one time it was expected that this welcome would be extended by Mr. Houston, who, because of his triple offices, as a member of President Wilson's cabinet, a Trustee of the Missouri Botanical Garden, and Chancellor of Washington University, as well as the grace with which he would have addressed you, would most suitably have performed this duty. Pressure of public work has prevented the Secretary of Agriculture from being with us, however, and I can only hope that you will feel that the welcome extended to you now carries with it as much cordiality and good will as if it came from an officer of the Government, the Garden, and the University.

Nothing could be more fitting at this time than some account of the life and work of the founder of this Garden, who deserves, both because of his far-sighted planning and his magnificent gift, to rank as America's foremost patron of botany. Most of you are no doubt familiar with the simple but impressive biographical facts concerning Mr. Shaw. How he came to this country from England with his father in 1818, being eighteen years of age, and after brief stays in Canada and New Orleans, settled in St. Louis. With a small stock of hardware he began business in one room, which also served as his bedroom and kitchen. From such a small beginning—and this on borrowed capital—scarcely more than twenty years were required by this pioneer merchant to amass a

fortune, for at forty years of age Mr. Shaw retired from active business to devote the remaining forty-nine years of his life to travel, and later to the active and remarkably intimate creation and management of a garden—that garden of which, because of his intelligent planning and unprecedented forethought and liberality, we are to-day celebrating the silver anniversary.

The advice and counsel of such men as Dr. George Engelmann, Sir William Hooker and Professor Asa Gray was freely sought and as freely given. In this connection I should like to read a letter from Sir Joseph Hooker, written June 17, 1888:

“The Camp, Sunnydale, England.

“My Dear Mr. Shaw:—

“I have just received your most handsome present of Engelmann's Botanical Works, edited by our dear late friend, Dr. Gray, and I do thank you most heartily, no less for your kind gift than for the effective service to botany that this most valuable contribution to the science renders. It is indeed a noble tribute to a man whose labors as a most conscientious and painstaking botanist have never been surpassed, and I prize it for the sake of the man whom I knew so well and esteemed so highly. I shall never forget my visit to him and to you and the afternoon I spent in your garden and museum at St. Louis, in company with Dr. and Mrs. Gray.

“I have been most interested in all that Dr. Gray told me last year about the noble botanical institution that you have founded and in his hopes that it would be a center of diffusion of knowledge, the influence of which would be felt far and wide.

“I think that he was more proud of your consulting him in the matter of its organization than of any of the many services which he had rendered to American botany, and he certainly regarded his labor with you as the most pleasant episode of his later years and by far the most important.

“Believe me, my dear sir, most faithfully and gratefully yours,

JOSEPH D. HOOKER.”

The country home of Mr. Shaw was built on these grounds in 1849, and the breaking of the prairie for his garden is said to have begun in 1857. There is no record of any formal opening of the Garden to the public, however, the date 1858 on the entrance of the main gate probably being the year it was erected rather than the time it was first opened to visitors. The small “Museum and Library,” as it is designated in the

stone over its entrance, was built in 1859, and this same year the installation of the Bernhardt Herbarium, previously purchased in Europe, marked Mr. Shaw's intention to make the Garden a center for scientific investigation and research. How successfully the founder of the Missouri Botanical Garden incorporated this idea in the document intended for the guidance of those who should administer this bequest, is evidenced by the remark of Judge Medill, one of the first members of the Board of Trustees, who, after the reading of the will, exclaimed: "That is a scientific institution and much should come of its services to botany!"

Mr. Shaw died August 25, 1889, and on September 10 the formal organization of the Board of Trustees, created by his will, took place. This is the anniversary we celebrate, for, as I have indicated, it is the only definite anniversary we have. Certainly as a "botanical institution, public in character," the Missouri Botanical Garden began its existence upon the organization of the trust declared by Mr. Shaw's will.

Two other notable bequests of Mr. Shaw require brief mention at this time, one indicating his desire for further scientific investigation in botany, the other the love for the beautiful in nature and his wish that all might have unlimited opportunity for acquiring and indulging this same passion. I refer, of course, to the endowment of the Henry Shaw School of Botany of Washington University, and the gift of Tower Grove Park to the city of St. Louis. The first is, owing to the broad-minded liberality of the Board of Trustees of the Garden and the untiring and unselfish efforts of its staff, taking a place among similar schools of the kind of which Mr. Shaw would not himself be ashamed. The latter, under the fatherly care of Mr. Gurney, its first and only Superintendent, whom we are proud to call the Head Gardener Emeritus of the Missouri Botanical Garden, is nobly fulfilling the purpose for which it was created.

It is proper, then, that this company of scholars should assemble here to do honor to the memory of Henry Shaw, to rejoice with us for the successful completion of twenty-five years of usefulness of the Missouri Botanical Garden.

Both personally and in my official capacity I welcome you not only to these ceremonies, but as coöperators in an era of even greater effort and achievement for the cause of the science which Mr. Shaw loved and honored and encouraged.

THE VEGETATION OF MONA ISLAND¹

N. L. BRITTON
New York Botanical Garden

During the progress of the scientific survey of Porto Rico, organized by the New York Academy of Sciences with the aid of the American Museum of Natural History, the New York Botanical Garden and Columbia University, in coöperation with the Porto Rican Insular Government, exploration has been carried out not alone on the mainland of Porto Rico but on several small islands adjacent and politically a part of that colony. Two of these islands lie in the Mona Passage between Porto Rico and Santo Domingo, and being scientifically almost unknown, were made points of examination in February, 1914, when I visited them in company with Mr. John F. Cowell, Director of the Buffalo Botanic Garden, Dr. Frank E. Lutz, Assistant Curator of Invertebrate Zoölogy in the American Museum of Natural History, and Mr. W. E. Hess, Plant Propagator of the Porto Rico Agricultural Experiment Station at Mayaguez. The trip was made in a sloop chartered at Mayaguez.

Desecheo Island, lying about eighteen miles northwest of Mayaguez, was first visited, and explored during two days; this island is somewhat more than one square mile in area, bordered by rocky coasts, rising abruptly into several hills, and covered with low trees and shrubs. Its flora is essentially identical with that of the drier parts of Porto Rico and of Santo Domingo; the small tree *Morisonia americana* and the snowy cactus (*Mamillaria nivosa*) have, however, not yet been found on the Porto Rican mainland, although both occur on the Island of Culebra east of Porto Rico, and neither of them is known on Santo Domingo. The cactus *Opuntia haitiensis*, plentiful there, is otherwise known only in Hispaniola, and the shrub *Torrubia discolor* of Hispaniola and Cuba has not been found on Porto Rico. The collection made

¹ Issued May 17, 1915.

by us on Desecheo, together with one made by Professor F. L. Stevens and Mr. W. E. Hess in May, 1913, shows that the spermatophytes of Desecheo number about 90 species; further intensive exploration might reveal a few more. A single species of fern was seen, four species of mosses, and two species of hepatics. As there is no probability of this little island ever having been a part of the Porto Rico mainland, its plants must have reached it by natural agencies; there are probably as many fungi and lichens as of other land plants collectively, so the total land flora of Desecheo probably includes at least 200 species.

Mona Island, lying about thirty miles to the southwest of Desecheo, in the middle of the Mona Passage between Santo Domingo and Porto Rico, has an area of approximately twenty square miles. Prior to our visit, only one botanical collection had been made there, when it was visited by Professor F. L. Stevens in 1913, at which time he obtained specimens of about 150 species of flowering plants, and gave especial attention to the parasitic fungi. The considerable land area of this island made a complete knowledge of its flora desirable, from the standpoint of geographical distribution of West Indian plants, and we were able to devote five days to collecting. The greater portion of Mona is a limestone plateau elevated from 125 to 175 feet, the surface of this plateau being nearly level and devoid of hills; its soil is very sparse, consisting altogether of reddish loam in depressions of the limestone surface, and not of considerable extent at any point visited by us. The limestone is evidently very porous, and there are no streams or ponds, and only a single spring was seen; the limestone is honeycombed with caves and caverns, some of them of considerable size. The rainfall is evidently considerable, but there are no records of its amount. Despite the paucity of soil, the whole plateau is rather densely covered with shrubs and low trees of a considerable number of species, their roots, for the most part, penetrating into crevices of the limestone. Herbaceous vegetation is restricted to comparatively few species. Eight species of cacti inhabit this plateau, and in places are very abundant, the snowy cactus

(*Mamillaria nivos*a) being more plentiful here than on any other island visited by us; *Opuntia Tayl*ori, hitherto known from Hispaniola, Culebra and the Virgin Islands, was found as a single colony; this has not yet been detected on the Porto Rican mainland.

The limestone plateau of Mona is bordered nearly throughout by steep escarpments and is accessible at but few points, except along the southwestern side, where there is a low plain several miles long and averaging about half a mile wide, from which the plateau is reached at a number of points over a talus of large limestone blocks. At the foot of the escarpment and of the talus on this southwestern side, the moistest conditions of Mona occur, and several species of trees here reach large size, notably the manchioneel (*Hippomane Mancinella*) and two species of *Ficus*. Here also grow two species of ferns, several bryophytes, and a number of *Polyporaceae* infesting dead wood. The soil of the narrow plain is more abundant than that of the plateau, permitting agricultural operations on a small scale and supporting a low forest made up of a considerable number of kinds of trees, with more herbaceous vegetation than exists on the plateau. Among rare elements of this vegetation are two orchids, *Domingoa hymenodes*, hitherto known from Hispaniola and Cuba, and *Ibidium lucayanum*, of Porto Rico, Anagada and the Bahamas. The coastal sands, which extend almost uninterruptedly along the shore of the plain, are inhabited by characteristic West Indian sand-dune species.

Lichens are quite abundant on tree trunks and on rocks of the talus, including a considerable number of species. Professor Lincoln W. Riddle has examined the collection and has submitted the following report upon them:

"The exploration of Mona Island has yielded 42 numbers of lichens, 40 collected by Dr. N. L. Britton, Messrs. J. F. Cowell and W. E. Hess, and 2 collected incidentally by Dr. F. L. Stevens. These 42 numbers represent 26 species in condition for determination.

"The species growing on the limestone rocks constitute the most striking and interesting part of the collection. These include four species of *Omphalaria*, a species of *Collema*, and a species of the *Dermatocarpaceae*, which is, unfortunately, sterile and, therefore, not further determinable. The omphalarias are all little known species.

O. polyglossa Nyl., collected from limestone rocks in Cuba by Charles Wright, and not otherwise known, is apparently common on Mona Island, as it is represented by two numbers, each with several well-developed specimens. There occur also *O. lingulata* Tuck., previously known from Cuba and Bermuda; a sterile omphalaria related to *O. Wrightii* Tuck., but apparently not identical; and one other species of the genus, probably new. It has not yet been possible to identify the species of *Collema*, and that may also prove to be new. Curiously enough, none of these calciphile species has yet been detected among the material collected in Porto Rico.

"In marked contrast to the rock-lichens, the bark-inhabiting lichens are all common species, widely distributed in Tropical America. The genus *Trypethelium* is best represented, with the species *T. Eluteriae* (four numbers), *T. ochroleucum*, and its variety *pallescens*, and *T. mastoideum* (two numbers). There are also such characteristic species as *Graphis Afzelii*, *Melanotheca cruenta*, *Pyrine picta*, *Physcia alba* and *P. speciosa*, *Parmelia sulphurata* and *P. tinctorum*, and *Ramalina complanata* and *R. Montagnei*. Probably owing to the comparatively unfavorable conditions on Mona Island, the foliose and fruticose lichens are mostly small specimens, not well-developed."

The total flora of flowering plants, as indicated by the collection made by Professor Stevens and our own, includes about 230 species; some of them are found only in cultivated grounds on the coastal plain and have probably been introduced by man. The total flora of land cryptogams is probably as great or greater than that of flowering plants, so we may conclude that the land flora of Mona consists of as high as 500 species. So far as the investigation of the collections has proceeded, the only apparent endemic species are a *Chamaesyce*, which Dr. C. F. Millspaugh has described as new, a *Tabebuia*, the description of which is herewith included, and two very interesting riccias, here described by Dr. Marshall A. Howe. One or more of the lichens may be undescribed. Further exploration in Porto Rico and in Hispaniola may very well reveal their presence on these larger islands. It is interesting to have ascertained that the flora of this isolated limestone island is not more highly specialized. It is not necessary, in my opinion, to assume a former land connection between Mona and either Porto Rico or Santo Domingo, because all its native species may readily have reached it through natural agencies.

I append a list of the species collected as thus far determined, and have indicated in this list their known distribution, except that of the lichens and *Uredinales*, as regards Porto Rico, Curacao, Hispaniola and the Bahamas, the nearest lands to Mona.

The names of new species, and new binomials, are printed in **heavy face type**.

LIST OF SPECIES INHABITING MONA ISLAND

MONOCOTYLEDONS

VALOTA INSULARIS (L.) Chase

Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas; Curacao.

SYNTHESISMA DIGITATUM (Sw.) Hitchc.

Frequent in cultivated ground, coastal plain: Porto Rico; Hispaniola; Bahamas.

PASPALUM CAESPITOSUM Fluegge

Frequent on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas.

PASPALUM SIMPSONI Nash

Collected by Professor Stevens, not found by us: Porto Rico; Bahamas.

PANICUM UTOWANAEUM Scribn.

Frequent on the coastal plain and on the plateau: Porto Rico; Desecheo; [Cuba; Guadeloupe].

PANICUM BARBINODE Trin.

Sandy soil, Playa de Fajaro: native of South America. Naturalized in the West Indies.

PANICUM ADSPERSUM Trin.

Moist soil, coastal plain: Porto Rico; Bahamas.

PANICUM MAXIMUM Jacq.

Frequent on the coastal plain: Native of tropical Africa; naturalized in the West Indies.

LASIACIS DIVARICATA (L.) Hitchc.

Frequent in thickets, coastal plain and plateau: Porto Rico; Hispaniola; Bahamas.

CHAETECHLOA SETOSA (Sw.) Scribn.

Frequent on the coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

CHAETECHLOA CAUDATA (Lam.) Scribn.

Occasional on the coastal plain: Desecheo; [Jamaica; Cuba; St. Thomas].

CHAETECHLOA IMBERBIS (Poir.) Scribn.

Frequent on the coastal plain: Porto Rico; Hispaniola; Bahamas.

CENCHROPSIS MYOSUROIDES (HBK) Nash

Frequent in cultivated ground on the coastal plain: Bahamas; Cuba.

CENCHRUS ECHINATUS L.

Common on the coastal plain and on sand dunes: Porto Rico; Hispaniola; Bahamas; Curacao.

CENCHRUS CAROLINIANUS Walt.

Collected by Professor Stevens, not found by us: Porto Rico; Hispaniola; Bahamas; Curacao.

ARISTIDA BROMOIDES HBK.

Common on the coastal plain: Porto Rico; Bahamas; Curacao.

SPOROBOLUS VIRGINICUS (L.) Beauv.

Common on coastal sands and on the coastal plain: Porto Rico; Hispaniola; Bahamas.

SPOROBOLUS ARGUTUS (Nees) Kunth

Frequent in moist soil on the coastal plain: Porto Rico; Hispaniola; Curacao.

CHLORIS PARAGUAIENSIS Steud.

Coastal plain, Sardinera: Porto Rico; Hispaniola; Bahamas; Curacao.

EUSTACHYS PETRAEA (Sw.) Desv.

Common on coastal sands and on the coastal plain: Porto Rico; Hispaniola; Bahamas.

ELEUSINE INDICA (L.) Gaertn.

Cultivated ground, coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

DACTYLOCTENIUM AEGYPTIUM (L.) Willd.

Cultivated ground, coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

PAPPOPHORUM LAGUROIDEUM Schrad.

Wet soil, coastal plain, between Sardinera and Ubero: Desecheo [Cuba; St. Eustatius].

ERAGROSTIS CILIARIS (L.) Link

Common on the coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

CYPERUS ELEGANS L.

Border of a marsh on the coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

CYPERUS TENUIS Sw.

Occasional on the coastal plain: Porto Rico; Hispaniola.

CYPERUS LIGULARIS L.

Marsh, Sardinera: Porto Rico; Hispaniola; Bahamas; Curacao.

CYPERUS BRUNNEUS Sw.

Common on coastal sands: Porto Rico; Bahamas; Hispaniola; Curacao.

FIMBRISTYLIS SPATHACEA Roth.

Common on the coastal plain: Porto Rico; Bahamas; Hispaniola.

SCLERIA LITHOSPERMA (L.) Sw.

Frequent on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas.

? *THRINAX PONCEANA* O. F. Cook

Apparently this species, but determined from leaves only. Rare in thickets on the coastal plain, and not found either in flower or in fruit: Porto Rico.

TILLANDSIA UTRICULATA L.

Common on trees and on rocks: Porto Rico; Hispaniola; Bahamas; Curacao.

TILLANDSIA RECURVATA L.

Common on trees and shrubs: Porto Rico; Hispaniola; Bahamas; Curacao.

CALLISIA REPENS L.

Occasional on the coastal plain and on the plateau: Porto Rico; Hispaniola; Curacao.

COMMELINA VIRGINICA L. (*C. elegans* HBK.)

Frequent on the coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

HYMENOCALLIS EXPANSA Herb.

Frequent in coastal sands. Determination from foliage only, therefore uncertain.

FURCRAEA TUBEROSA Ait. f.

Coastal plain between Sardinera and Ubero; probably introduced from Porto Rico. Determined from leaf specimens only: Porto Rico.

IBIDIUM LUCAYANUM Britton

Low woods, coastal plain near Sardinera: Porto Rico; Bahamas.

EPIDENDRUM PAPILIONACEUM Vahl

Common on shrubs and on the ground, coastal plain and plateau: Porto Rico; Hispaniola; recorded from the Bahamas.

DOMINGOA HYMENODES (Rehb. f.) Schltr.

On small trees between Sardinera and Ubero: Hispaniola [Cuba].

DICOTYLEDONS

PEPEROMIA HUMILIS (Vahl) A. Dietr.

Shaded limestone rocks near Sardinera. Plants with only the upper leaves opposite: Porto Rico; Hispaniola.

CELTIS TRINERVIA Lam.

Base of cliffs, Sardinera: Porto Rico; Hispaniola.

FICUS LAEVIGATA Vahl

Coastal plain and plateau; largest at the bases of cliffs: Porto Rico; Hispaniola.

FICUS STAHLII Warb.

Frequent along the bases of cliffs, eastern edge of the coastal plain. Trees up to 12 m. high. Determined from foliage only: Porto Rico.

CHLOROPHORA TINCTORIA (L.) Gaud.

Base of cliffs, Sardinera: Porto Rico; Hispaniola.

PILEA TRIANTHEMOIDES (Sw.) Lindl.

Frequent on the coastal plain: Porto Rico.

PILEA MICROPHYLLA (L.) Liebm.

Occasional on the plateau: Porto Rico; Hispaniola; Bahamas; Curacao.

COCCOLOBIS UVIFERA (L.) Jacq.

Common on coastal sands and rocks: Porto Rico; Hispaniola; Bahamas; Curacao.

COCCOLOBIS OBTUSIFOLIA Jacq.

Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; ? Bahamas.

COCCOLOBIS LAURIFOLIA Jacq.

Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas.

COCCOLOBIS NIVEA Jacq.

Base of cliff, Sardinera: Porto Rico; Hispaniola.

AMARANTHUS TRISTIS L.

Waste and cultivated grounds on the coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

ACHYRANTHES INDICA (L.) Mill.

Frequent in cultivated ground, coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

LITHOPHILA MUSCOIDES Sw.

Collected by Professor Stevens, not found by us: Porto Rico; Hispaniola; Bahamas; Curacao.

CELOSIA NITIDA Vahl

Frequent on the coastal plain: Porto Rico; Hispaniola; Bahamas.

MIRABILIS JALAPA L.

Waste grounds, uncommon: Porto Rico; Hispaniola; Bahamas.

BOERHAAVIA COCCINEA Mill.

Common on the coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

? PISONIA SUBCORDATA Sw.

Base of cliffs, Sardinera. Trees, 12 m. high or more, barren at the time of our visit and determination therefore uncertain: Porto Rico.

RIVINA HUMILIS L.

Common on the coastal plain on the plateau: Porto Rico; Hispaniola; Bahamas; Curacao.

TRICHOSTIGMA OCTANDRUM (L.) H. Walt.

Frequent on the talus, vicinity of Sardinera, forming vines 20 m. long with trunks up to 1.5 dm. diameter: Porto Rico; Hispaniola.

PETIVERIA ALLIACEA L.

Occasional in thickets on the coastal plain: Porto Rico; Hispaniola; Bahamas.

SESUVIUM PORTULACASTRUM L.

Common on coastal rocks and sands: Porto Rico; Hispaniola; Bahamas; Curacao.

TALINUM PANICULATUM (Jacq.) Gaertn.

Coastal plain, Sardinera: Porto Rico; Hispaniola.

PORTULACA PHAEOSPERMA Urban

Moist soil, coastal plain and plateau: Porto Rico; Hispaniola; Bahamas; Curacao.

PORTULACA OLERACEA L.

Sandy soil, Playa de Fajaro: Porto Rico; Hispaniola; Bahamas; Curacao.

NECTANDRA CORIACEA (Sw.) Griseb.

Base of limestone cliff, Sardinera: Porto Rico; Hispaniola; Bahamas; Curacao.

CASSYTHA AMERICANA Nees

Frequent on the coastal plain: Porto Rico; Hispaniola; Bahamas.

CLEOME GYNANDRA L.

Waste and cultivated grounds, coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

CAPPARIS CYNOPHALLOPHORA L. (*C. jamaicensis* Jacq.)

Frequent on the coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

CAPPARIS FLEXUOSA L. (*C. cynophallophora* Jacq.)

Common on the coastal plain: Porto Rico; Hispaniola; Bahamas.

LEPIDIUM VIRGINICUM L.

Common in waste and cultivated ground: Porto Rico; Hispaniola; Bahamas.

BRASSICA INTEGRIFOLIA (West) O. E. Schulz

Occasional in cultivated ground, coastal plain: Porto Rico; Bahamas.

CAKILE LANCEOLATA (Willd.) O. E. Schulz

Common on coastal sands: Porto Rico; Hispaniola; Bahamas.

PITHECOLOBIUM UNGIUS-CATI (L.) Benth.

Common in coastal thickets and occasional on the coastal plain. All specimens examined were spineless: Porto Rico; Hispaniola; Bahamas; Curacao.

CASSIA OCCIDENTALIS L.

Sandy soil, Playa de Fajaro: Porto Rico; Hispaniola; Bahamas.

CHAMAECRISTA GRANULATA (Urban) Britton. (*Cassia portoricensis granulata* Urban.)

Common on the coastal plain and on sand dunes: Porto Rico.

CHAMAECRISTA DIFFUSA (DC.) Britton. (*Cassia diffusa* DC.)

Collected by Professor Stevens, not found by us: Porto Rico; Curacao.

? CAESALPINIA DOMINGENSIS Urban

On the plateau, Sardinera. Determined from description: Hispaniola.

GUILANDINA CRISTA (L.) Small

Occasional in coastal thickets: Porto Rico; Hispaniola; Bahamas.

GUILANDINA MELANOSPERMA (Urban) Britton. (*Caesalpinia melanosperma* Urban.)

Frequent on the coastal plain: St. Croix.

GUILANDINA DIVERGENS (Urban) Britton

Frequent on the coastal plain: Culebra [St. Thomas].

KRAMERIA IXINA L.

Occasional on the coastal plain and on the plateau: Porto Rico; Hispaniola; Curacao.

INDIGOFERA SUFFRUTICOSA Mill

Cultivated ground, coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

CRACCA CINEREA (L.) Morong

Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas; Curacao.

STYLOSANTHES HAMATA (L.) Taub.

Frequent on the coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

MEIBOMIA SUPINA (Sw.) Britton

Frequent on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas; Curacao.

MEIBOMIA MOLLIS (Vahl) Kuntze

Occasional in cultivated ground on the coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

BRADBURYA VIRGINIANA (L.) Kuntze

Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas.

GALACTIA STRIATA (Jacq.) Urban

Frequent on the coastal plain and on the plateau. A race with small leaflets and slender-peduncled racemes: Porto Rico; Hispaniola.

CANAVALLIA LINEATA (Thunb.) DC.

Common on coastal sands: Porto Rico; Hispaniola; Bahamas.

? DOLICHOLUS MINIMUS (L.) Medic

Cultivated ground, Ubero. A race apparently of this species, with thick leaflets, strongly veined; not found either in flower or in fruit, the determination, therefore, uncertain.

DOLICHOLUS RETICULATUS (Sw.) Millsp.

Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas.

ERYTHROXYLON AREOLATUM L.

Frequent on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas.

GUAIAACUM SANCTUM L.

Frequent on the coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

ZANTHOXYLUM PUNCTATUM Vahl

Coastal plain between Sardinera and Ubero: Porto Rico; Hispaniola.

AMYRIS ELEMIFERA L.

Occasional on the coastal plain: Porto Rico; Hispaniola; Bahamas.

SURIANA MARITIMA L.

Common on coastal sands: Porto Rico; Hispaniola; Bahamas; Curacao.

ELAPHRIUM SIMARUBA (L.) Rose

Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas; Curacao.

STIGMAPHYLLON LINGULATUM (Poir.) Small

Common on the coastal plain and on the plateau: Porto Rico; Hispaniola.

BYRSONIMA LUCIDA (Sw.) L. C. Rich

Occasional on the coastal plain: Porto Rico; Hispaniola; Bahamas.

XYLOPHYLLA EPIPHYLLANTHUS (L.) Britton. (*Phyllanthus Epiphyllanthus* L.)

Common on the coastal plain: Porto Rico; Hispaniola; Bahamas.

PHYLLANTHUS NIRURI L.

Cultivated ground, coastal plain. Not collected: Porto Rico; Hispaniola; Bahamas; Curacao.

CROTON LUCIDUS L.

Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas.

CROTON DISCOLOR Willd.

Common on the plateau: Porto Rico; Hispaniola.

CROTON BETULINUS Vahl

Common on the coastal plain and on the plateau: Porto Rico; Hispaniola.

ARGITHAMNIA CANDICANS Sw.

Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas; Curacao.

RICINUS COMMUNIS L.

Waste grounds, Ubero: Native of the Old World tropics.

HIPPOMANE MANCINELLA L.

Common on the coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

CHAMAESYCE MONENSIS Millsp.

Limestone plateau, Ubero: Endemic.

CHAMAESYCE PORTORICENSIS (Urban) Millsp.

On limestone rocks, Ubero and Sardinera: Porto Rico.

CHAMAESYCE SERPENS (HBK.) Small

Moist soil, coastal plain and plateau: Porto Rico.

CHAMAESYCE HYPERICIFOLIA (L.) Millsp.

Common in cultivated ground on the coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

CHAMAESYCE BUXIFOLIA (Lam.) Small

Common on coastal sands: Porto Rico; Hispaniola; Bahamas; Curacao.

AKLEMA PETIOLARIS (Sims) Millsp. (*Euphorbia petiolaris* Sims.)

Common on the coastal plain and on the plateau: Porto Rico.

POINSETTIA HETEROPHYLLA (L.) Kl. & Garcke

Sandy beach, Playa de Fajaro: Porto Rico; Hispaniola; Bahamas.

PEDILANTHUS LATIFOLIUS Millsp. & Britton, sp. nov.

Shrubby, about 6 feet high, the young branches zig-zag, puberulent. Leaves ovate to ovate-orbicular, 4.5 inches long or less, very nearly sessile, dull-green, acute at the apex, roundish or subcordate at the base, very inconspicuously veined, glabrous, the midrib elevated but not keeled beneath. Inflorescence terminal, cymose, puberulent, bracteate; bracts lanceolate, acute, 3.5–4 x 2 lin., somewhat exceeding the peduncles; involucre about 10 x 4.5 lin., glabrous without and within, tube narrow anteriorly, main lobes lanceolate-oblong, rounded obtuse, ciliate at the apex, the accessory lobes equal or nearly so connivent with the main lobes to near the ciliate apices, fifth lobe elongate-ligulate, truncate ciliate, somewhat shorter than the accessory lobes and nearly closing the superior fissure of the tube; appendix large, strongly saccate, about one-third the length of the tube, split for half its length into two sarcous, ligulate slightly grooved and emarginate lobes; glands 4, of two sorts: the upper pair reniform at the summit of a broadly triangular stipe which is connivent with the surface of the appendix, anterior margins free and sharp; lower pair about one-half the size of the upper, discoid, peltate on a very short, free pedicel. Male pedicels numerous, glabrous; female pedicel glabrous; ovary glabrous; style 3-lobed at the apex, the stigmatic branches bifid. Fruit unknown.

Castle Point, Bermuda (*Brown & Britton, 820, TYPE*). Near Bath, Jamaica (*Britton, 3491*). Baracoa, Cuba (*Bemis*). Sanchez, Santo Domingo (*Rose, Fitch & Russell, 4397*). Mona Island (*Britton, Cowell & Hess, 1786*). Perhaps indigenous at the Santo Domingo locality cited; at all the others an evident escape from cultivation, or in gardens.

METOPIMUM TOXIFERUM (L.) Krug & Urban

Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas.

COMOCLADIA DODONAEA (L.) Urban

Frequent on the plateau: Porto Rico; Hispaniola.

RHACOMA CROSSOPETALUM L.

Frequent on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas; Curacao.

GYMINDA LATIFOLIA (Sw.) Urban

Occasional on the coastal plain: Porto Rico; Hispaniola; Bahamas.

SCHAEFFERIA FRUTESCENS Jacq.

Common on the coastal plain: Porto Rico; Hispaniola; Bahamas.

CARDIOSPERMUM MICROCARPUM HBK.

Frequent on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas.

HYPELATE TRIFOLIATA Sw.

Coastal plain near Sardinera: Porto Rico; Hispaniola; Bahamas.

EXOTHEA PANICULATA (Juss.) Radlk.

Base of limestone cliffs, Sardinera: Porto Rico; Hispaniola; Bahamas.

DODONAEA EHRENBERGII Schl.

Common on the coastal plain and on the plateau: Hispaniola; Bahamas.

KRUGIODENDRON FERREUM (Vahl) Urban

Occasional on the coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

REYNOSIA UNCINATA Urban

Frequent on the plateau: Porto Rico.

SARCOMPHALUS TAYLORI Britton

Occasional on the coastal plain: Bahamas.

COLUBRINA COLUBRINA (L.) Millsp.

Occasional along the base of the cliffs, coastal plain: Porto Rico; Hispaniola; Bahamas.

CISSUS TRIFOLIATA L.

Coastal thickets: Porto Rico; Hispaniola; Bahamas; Aruba.

CORCHORUS SILIQUOSUS L.

Occasional on the coastal plain: Porto Rico; Hispaniola; Bahamas.

CORCHORUS HIRSUTUS L.

Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas; Curacao.

ABUTILON UMBELLATUM (L.) Sweet

Frequent on the coastal plain: Porto Rico; Hispaniola; Curacao.

GAYOIDES CRISPUM (L.) Small

Occasional on the coastal plain: Porto Rico; Hispaniola; Bahamas.

MALVASTRUM SPICATUM (L.) A. Gray

Cultivated ground, coastal plain: Porto Rico; Hispaniola; Curacao.

SIDA SPINOSA L.

Cultivated ground, coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

SIDA GLABRA Mill. (*S. ulmifolia* Cav.)

Frequent on the coastal plain: Porto Rico; Hispaniola.

SIDA PROCUMBENS Sw.

Occasional on the coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

SIDA ACUMINATA DC.

Frequent on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas.

BASTARDIA VISCOSA (L.) HBK.

Occasional on the coastal plain: Porto Rico; Hispaniola; Bahamas; recorded from Curacao.

MALACHRA CAPITATA L.

Occasional in cultivated ground, coastal plain: Porto Rico; Hispaniola.

PARITUM TILIACEUM (L.) Juss.

Border of a swamp, Sardinera: Porto Rico; Hispaniola; Bahamas.

GOSSYPIUM BARBADENSE L.

Spontaneous after cultivation on the coastal plain. Apparently not native.

MELOCHIA TOMENTOSA L.

Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas; Curacao.

WALTHERIA AMERICANA L.

Occasional on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas; Curacao.

AYENIA PUSILLA L.

Frequent on the coastal plain: Porto Rico; Hispaniola; Bahamas.

HELICTERES JAMAICENSIS Jacq.

Frequent on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas.

CLUSIA ROSEA Jacq.

Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas.

CANELLA WINTERANA (L.) Gaertn.

Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas.

TURNERA DIFFUSA Willd.

Occasional on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas.

PASSIFLORA SUBEROSA L.

Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas; Curacao.

PASSIFLORA FOETIDA L.

Sandy beach, Playa de Fajaro: Porto Rico; Hispaniola; Bahamas; Curacao.

CARICA PAPAYA L.

Common on the coastal plain about Sardinera, apparently established after cultivation. A race with small globose fruits. Original home unknown.

HARRISIA PORTORICENSIS Britton

Common on the talus and on the plateau: Porto Rico.

CEPHALOCEREUS ROYENI (L.) Britton & Rose

Common on the plateau: Porto Rico [St. Thomas to Antigua].

CACTUS INTORTUS Mill. (*Melocactus portoricensis* Suringar.)

Common on the plateau: Porto Rico [St. Thomas to Antigua].

CORYPHANTHA NIVOSA (Link) Britton. (*Mamillaria nivosa* Link.)

Very abundant on the plateau: Culebra [St. Thomas to Tortola; Antigua]; Bahamas.

OPUNTIA CATACANTHA Link & Otto

Common on the plateau; occasional on the coastal plain: Porto Rico [St. Thomas to Antigua].

OPUNTIA TAYLORI Britton

Top of cliff near Sardinera: Santo Domingo; Culebra [St. Thomas to Tortola].

OPUNTIA DILLENII (Ker.) Haw.

Common on the coastal plain and on the plateau. Not collected: Porto Rico; Hispaniola; Bahamas.

TERMINALIA CATAPPA L.

Occasional on coastal sands: Porto Rico; Hispaniola; [spontaneous after cultivation in the Bahamas].

CONOCARPUS ERECTA L.

Occasional in coastal sands: Porto Rico; Hispaniola; Bahamas; Curacao.

BUCIDA BUCERAS L.

Coastal woods, Ubero: Porto Rico; Hispaniola; Bahamas.

LAGUNCULARIA RACEMOSA (L.) Gaertn.

Borders of marshes, coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

CALYPTRANTHES PALLENS (Poir.) Griseb.

Base of cliffs, Ubero: Porto Rico (?); Hispaniola; Bahamas.

EUGENIA BUXIFOLIA (Sw.) Willd.

Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas.

EUGENIA AXILLARIS (Sw.) Willd.

Frequent or occasional on the coastal plain, at the base of cliffs and on the plateau: Porto Rico; Hispaniola; Bahamas.

EUGENIA RHOMBEA (Berg.) Krug. & Urban

Coastal plain between Sardinera and Ubero: Porto Rico; Hispaniola; Bahamas.

ANANOMIS FRAGRANS (Sw.) Griseb.

Occasional on the coastal plain: Porto Rico; Hispaniola. Recorded from the Bahamas.

JACQUINIA BARBASCO (Loefl.) Mez.

Common in coastal thickets and occasional on the coastal plain: Porto Rico; Hispaniola; Curacao.

? DIPHOLIS

Coastal plain, Sardinera. A tree about 12 m. high, in foliage only.

BUMELIA OBOVATA (Lam.) DC.

Frequent on the coastal plain. Not in flower or fruit at the time of our visit: Porto Rico; Hispaniola; Curacao.

PLUMIERA OBTUSA L.

Common on the coastal plain and on the plateau: Hispaniola; Bahamas.

RAUWOLFIA TETRAPHYLLA L. (*R. nitida* Jacq.)

Frequent on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas.

ECHITES AGGLUTINATA Jacq.

Occasional on the coastal plain and on the plateau: Porto Rico; Hispaniola.

URECHITES LUTEA (L.) Britton

Occasional on the coastal plain: Porto Rico; Hispaniola; Bahamas.

METASTELMA (undetermined)

Coastal rocks, Ubero.

METASTELMA (undetermined)

Occasional on the coastal plain and on the plateau.

EVOLVULUS GLABER Spreng.

Moist soil, coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

JACQUEMONTIA JAMAICENSIS (Jacq.) Hall. f.

Occasional on coastal sands: Porto Rico; Hispaniola; Bahamas.

JACQUEMONTIA PENTANTHA (Jacq.) D. Don

Frequent on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas; Curacao.

OPERCULINA AEGYPTIA (L.) House

Cultivated ground, coastal plain: Porto Rico; Hispaniola; Curacao.

? EXOGONIUM MICRODACTYLUM (Griseb.) House

Occasional on the plateau. Specimen insufficient for certain determination.

IPOMOEA PES-CAPRAE (L.) Roth.

Common on coastal sands: Porto Rico; Hispaniola; Bahamas; Curacao.

IPOMOEA TRILOBA L.

Frequent in cultivated ground on the coastal plain: Porto Rico; Bahamas.

CALONYCTION GRANDIFLORUM (Jacq.) Choisy. (*Ipomoea tuba* G. Don.)

Frequent in coastal thickets: Porto Rico; Hispaniola; Bahamas; Curacao.

VARRONIA GLOBOSA Jacq.

Occasional on the coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

BOURRERIA SUCCULENTA Jacq.

Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Curacao.

MALLOTONIA GNAPHALODES (L.) Britton.¹ (*Tournefortia gnaphalodes* R. Br.)

Common on coastal sands: Porto Rico; Hispaniola; Bahamas; Curacao.

TOURNEFORTIA HIRSUTISSIMA L.

Base of limestone cliffs, Sardinera: Porto Rico; Hispaniola.

TOURNEFORTIA MICROPHYLLA Bert.

Common on the coastal plain and on the plateau: Porto Rico; Hispaniola.

HELIOTROPIUM CRISPIFLORUM Urban

Moist soil, coastal plain: Porto Rico. Closely resembles the Porto Rico plant but is lower and with shorter internodes; no flowering specimens were obtained.

HELIOTROPIUM PARVIFLORUM L.

Frequent on the coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

LANTANA SCABRIDA Ait.

Collected by Professor Stevens, not found by us: Porto Rico; Hispaniola. Apparently specifically distinct from *L. Camara* L.

LANTANA INVOLUCRATA L.

Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas; Curacao.

VALERIANODES JAMAICENSIS (L.) Medic

Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas; Curacao.

VALERIANODES STRIGOSA (Vahl) Kuntze

Frequent on the coastal plain and on the plateau: Porto Rico; Hispaniola.

¹*Mallotonia* (Griseb.) Britton, gen. nov.

Tournefortia Section *Mallotonia* Griseb. Fl. Brit. W. I. 483. 1861.

Type species: *Tournefortia gnaphalodes* (L.) R. Br.

SALVIA SEROTINA L. (*S. micrantha* Vahl)

Frequent on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas.

HYPTIS PECTINATA (L.) Poit.

Cultivated ground on the coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

SOLANUM NIGRUM L. (*S. americanum* Mill.)

Cultivated ground, Sardinera: Porto Rico; Hispaniola; Bahamas; Curacao.

SOLANUM VERBASCIFOLIUM L.

Occasional at the bases of cliffs and on the coastal plain: Porto Rico; Hispaniola; Bahamas.

BRAMIA MONNIERIA (L.) Drake. (*Herpestis Monniera* HBK.)

Border of a pool, Sardinera: Porto Rico; Hispaniola; Bahamas.

CAPRARIA BIFLORA L.

Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas; Curacao.

SCOPARIA DULCIS L.

In moist soil on the coastal plain: Porto Rico; Hispaniola; Bahamas.

TABEBUIA HETEROPHYLLA (DC.) Britton. (*Raputia* (?) *heterophylla* DC.; *Tabebuia triphylla* DC., not *Bignonia triphylla* L.)

Frequent on the coastal plain and on the plateau. Leaves 1-foliate to 5-foliate: Porto Rico.

TABEBUIA LUCIDA Britton, sp. nov.

A tree up to 5 m. high. Leaves 3-5-foliate; petioles slender, lepidote, 6 cm. long or less; petiolules of the larger, upper leaflets slender, lepidote, 8-20 mm. long; lower leaflets sessile or nearly so; leaflets thin-coriaceous, narrowly oblong or oblong-ob lanceolate, 5-10 cm. long, 1-3 cm. wide, shining, reticulate-veined and lepidote on both sides, rather abruptly acute or obtusish at the apex, narrowed or obtuse at the base; flowers clustered; pedicels lepidote; calyx about 14 mm. long, 2-lipped; corolla pink, glabrous, about 5 cm. long, its cylindric tube 5-6 mm. long, its narrowly campanulate throat about 3 cm. long, its limb about 1.5 cm. long, the lobes nearly entire.

Limestone cliffs, Sardinera, Mona Island, Porto Rico (*Britton, Cowell and Hess, 1686*).

SESAMUM ORIENTALE L.

Cultivated ground, coastal plain. Native of the East Indies.

BLECHUM BROWNEI Juss.

Shaded rocks, Sardinera: Porto Rico; Hispaniola; Bahamas.

JUSTICIA PERIPLÔCIFOLIA Jacq.

Occasional on the coastal plain, a narrow-leaved race: Porto Rico; Hispaniola.

JUSTICIA PECTORALIS Jacq.

Border of pool, Sardinera: Porto Rico; Hispaniola.

PLANTAGO MAJOR L.

Cultivated ground, coastal plain. Not collected. Native of the Old World.

EXOSTEMA CARIBAEUM (Jacq.) R. & S.

Frequent on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas.

RANDIA ACULEATA L.

Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas; Curacao.

GUETTARDA ELLIPTICA Sw.

Occasional on the coastal plain: Porto Rico; Hispaniola; Bahamas.

STENOSTOMUM ACUTATUM DC.

Frequent on the coastal plain and on the plateau: Porto Rico; Curacao.

ERITHALIS FRUTICOSA L.

Common on sand dunes, on the coastal plain and occasional on the plateau: Porto Rico; Hispaniola; Bahamas; Curacao.

CHIOCOCCA ALBA (L.) Hitchc.

Occasional on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas.

STRUMPFIA MARITIMA Jacq.

Limestone plateau near Ubero, frequent: Porto Rico; Hispaniola; Bahamas; Curacao.

PSYCHOTRIA UNDATA Jacq.

Occasional on the coastal plain: Porto Rico; Hispaniola; Bahamas.

ERNODEA LITTORALIS Sw.

Common on coastal sands: Porto Rico; Hispaniola; Bahamas; Bonaire.

SPERMACOCE TENUIOR L.

Frequent on the coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

CUCUMIS ANGURIA L.

Cultivated ground, Sardinera: Porto Rico; Hispaniola; Curacao.

EUPATORIUM ODORATUM L.

Common on the coastal plain: Porto Rico; Hispaniola; Bahamas.

EUPATORIUM ATRIPLICIFOLIUM Lam.

Coastal rocks, Sardinera: Porto Rico; recorded from Hispaniola and from the Bahamas.

LEPTILON PUSILLUM (Nutt.) Britton

Common in waste and cultivated grounds, coastal plain: Porto Rico; Hispaniola (?); Bahamas.

LEPTILON BONARIENSE (L.) Small

Cultivated ground, Sardinera: Porto Rico; Hispaniola.

PLUCHEA PURPURASCENS (Sw.) DC.

Borders of marshes, coastal plain: Porto Rico; Hispaniola; Bahamas.

BORRICHIA ARBORESCENS (L.) DC.

Occasional on coastal rocks: Porto Rico; Hispaniola; Bahamas.

WEDELIA PARVIFLORA L. C. Rich

Common on the coastal plain: Porto Rico.

ELEUTHERANTHERA RUDERALIS (Sw.) Sch. Bip.

Cultivated ground, coastal plain: Porto Rico; Hispaniola. Erroneously recorded from the Bahamas.

BIDENS CYNAPIIFOLIA HBK.

Collected by Professor Stevens, not found by us: Porto Rico; Hispaniola; Bahamas; Curacao.

PTERIDOPHYTA

(Determined by Miss Margaret Slosson)

ADIANTUM FRAGILE Sw.

Limestone cliff, Sardinera: Porto Rico; Hispaniola.

ACROSTICHUM AUREUM L.

Border of pool near Sardinera. Determined from barren leaf specimen:
Porto Rico; Hispaniola; Bahamas; Curacao.

CYCLOPELTIS SEMICORDATA (Sw.) J. Smith

Shaded limestone rocks, Sardinera: Porto Rico; Hispaniola.

MUSCI

(Determined by Elizabeth G. Britton and R. S. Williams)

THUIDIUM INVOLVENS (Hedw.) Mitt.

On dead wood and shaded rocks: Porto Rico; Hispaniola.

TORTULA AGRARIA Sw.

On the ground near Sardinera: Porto Rico; Hispaniola; Bahamas.

HYOPHILA GUADELUPENSIS Broth.

Wet soil on the coastal plain between Sardinera and Ubero: Guadeloupe; Montserrat.

BRYUM MICRODECURRENS E. G. Britton

Wet soil on the coastal plain between Sardinera and Ubero: St. Thomas.

CALYMPERES RICHARDI C. Muell.

On tree trunks, base of cliff, Sardinera: Porto Rico; Hispaniola; Bahamas.

CALYMPERES (an apparently undescribed species)

On *Bourreria*, Ubero; Hispaniola.

HEPATICAEE

JUNGERMANNIACEAE

(Determined by Professor A. W. Evans)

BRACHIOLEJEUNEA BAHAMENSIS Evans

On limestone, Ubero; on trunk of *Gymnanthes*, Sardinera: Bahamas.

MASTIGOLEJEUNEA AURICULATA (Wils. & Hook.) Schiffn.

On shaded limestone and on dead wood, Sardinera: Porto Rico; Bahamas.

LEJEUNEA (barren and undeterminable)

On shaded limestone, bark and dead wood.

FRULLANIA SQUARROSA (R. B. & U.) Dumort.

On trunks and logs on the coastal plain: Porto Rico; Bahamas.

FRULLANIA (barren and undeterminable)

On dead wood, Sardinera.

RICCIACEAE

(Contributed by Dr. Marshall Avery Howe)

RICCIA BRITTONII, sp. nov.

Thallus simple or once dichotomous, forming irregularly gregarious patches, oblong-ovate, linguiform, or obovate, 2-5 mm. x 1-2 mm., subacute or obtuse, conspicuously alveolate-reticulate and light green above, with a scarious-albescent border 80-175 μ wide, concolorous or very commonly brownish laterally and ventrally; median sulcus deep and acute except in older parts; ventral scales small, inconspicuous, hyaline, rarely exceeding the thin membranous ascending thallus-margins; transverse sections mostly 1.5-2.0 times as wide as high, the ventral outlines semi-orbicular in younger parts, becoming flattened in the older; cells of the primary dorsal epidermis cylindric dome-shaped or subhemispheric, soon collapsing, leaving shallow slightly indurated more or less persistent cup-like vestiges; monoecious; antheridial ostioles scarcely elevated; spores brown, becoming subopaque, soon exposed, 100-145 μ in maximum diameter, rather ob-

scurely or sometimes distinctly angled, often flattened, destitute of wing-margins, almost uniformly areolate over the whole surface, with age showing in profile obtuse or truncate papillae 3–5 μ long, areolae mostly 10–18 μ wide.

On wet, sunny soil, accompanied by *R. violacea*, between Sardinera and Ubero, Mona Island, February, 1914, Britton, Cowell, & Hess, 1749a.

Riccia Brittonii exhibits certain points of contact with *Riccia sorocarpa* Bisch. and *R. dictyospora* M. A. Howe.¹ It is close to *R. sorocarpa* in vegetative characters, though differing in the wider, more pronounced, scarious-albescent thallus-margins and slightly in the character of the epidermis, but it departs widely from this species in the spores, which are much larger (100–145 μ vs. 70–90 μ , max. diam.), are destitute of wing-margins, and commonly have the areolae of the inner faces almost as well and regularly developed as those of the outer face. From *Riccia dictyospora*, the species differs in the less elongate thallus (2–5 mm. vs. 4–10 mm.), the albescent instead of dark purple thallus-margins and scales, the more semicircular and less parabolic outlines of transverse sections of the thallus, and in the larger spores (100–145 μ vs. 95–116 μ , max. diam.), with larger areolae (10–18 μ vs. 8–12 μ .

RICCIA VIOLACEA, sp. nov.

Thallus simple or 1–3 times dichotomous, irregularly gregarious, 1.5–4.0 mm. long, the main segments oblong-obovate or linguiform, 0.65–1.15 mm. broad, rather obscurely and finely areolate and dark green above, dark violet or blackish at margins and on sides, this color encroaching on the surface here and there, especially in the older parts and at the sinuses; median sulcus shallow or obsolete except at apex; ventral scales very short or rudimentary, dark violet, rarely overlapping, commonly divided into a series of small irregular often tooth-like lamellae, each consisting of only a few cells; transverse sections plano-convex, somewhat flattened-semiorbicular, or occasionally biconvex, 1.5–2.0 times as wide as high; the margins obtuse or rounded, bearing especially toward the apex numerous or occasional violet or sometimes hyaline conic or subcylindric acute or obtuse papillae 30–110 μ long and 25–45 μ broad at base; cells of the primary dorsal epidermis subhemispheric or mammiform, soon collapsing and leaving inconspicuous vestigia; remaining parts unknown.

On wet, sunny soil, accompanied by *Riccia Brittonii*, between Sardinera and Ubero, Mona Island, February, 1914, Britton, Cowell, & Hess, 1749b.

In size, habit, and color, *R. violacea* is somewhat suggestive of *R. nigrella* DC., but the thallus has papillae or very short cilia at the margins, which are wanting in *R. nigrella*, the scales are much smaller, more rudimentary and more divided than in *R. nigrella*, and the cells of the primary epidermis are much less persistent. Its nearest affinity is doubtless with *R. atromarginata* Levier, which is known from Sicily, Sardinia, and Greece; from this it appears to differ (if one may judge from the descriptions alone) in the obtuse thallus-margins, the very short, rudimentary, divided, rarely overlapping scales, and the commonly violet papillae which are confined to the margins and sides while in *R. atromarginata* the hyaline incurved "pili" are said to cover also the anterior dorsal surface.

LICHENES

(Determined by Professor Lincoln W. Riddle)

ARTHOPYRENIA

On *Coccolobis obtusifolia*, Ubero.

PYRENULA

On bark, Sardinera.

MELANOTHECA CRUENTA (Mont.) Muell. Arg.

On *Gymnanthes*, Sardinera.

TRYPETHELIUM ELUTERIAE Spreng.

On *Pithecolobium*, Sardinera, and on *Coccolobis obtusifolia*, Ubero.

¹Bull. Torr. Bot. Club 28: 163. 1901.

TRYPETHELIUM MASTOIDEUM Ach.

On *Pithecolobium*, Sardinera.

TRYPETHELIUM OCHROLEUCUM Nyl.

On *Zanthoxylum*, between Sardinera and Ubero.

OPEGRAPHIA

On *Ficus*, Sardinera; on *Calyptranthes*, Ubero.

GRAPHIS AFZELII Ach.

On *Zanthoxylum*, between Sardinera and Ubero; on *Pithecolobium*, Sardinera.

GRAPHIS

Collected by Professor Stevens.

CHIODECTON

On *Plumiera*, Sardinera.

LEPTOTREMA

On dead wood, Sardinera.

CLADONIA FIMBRIATA var. CONIOCRAEA (Floerke) Wainio

On dead log, Sardinera.

OMPHALARIA LINGULATA Tuck.

On limestone, Sardinera.

OMPHALARIA POLYGLOSSA Nyl.

On exposed limestone, Ubero.

OMPHALARIA

On limestone, Ubero.

COLLEMA

On limestone rocks, Sardinera.

LEPTOGIUM (sterile and indeterminable)

On *Torrubia*, Sardinera.

PARMELIA TINCTORUM Despv.

On a tree trunk.

PARMELIA SULPHURATA Nees and Flot.

On a dead log, Sardinera.

RAMALINA MONTAGNEI De Not.

On a twig, Sardinera. Collected also by Professor Stevens.

RAMALINA COMPLANATA (Sw.) Ach.

On a twig, Sardinera.

PYXINE PICTA (Sw.) Tuck.

On *Pithecolobium*, Sardinera; on *Zanthoxylum*, between Sardinera and Ubero.

PHYSCIA SPECIOSA (Wulf.) Nyl. (A small form)

On *Ficus*, Sardinera.

PHYSCIA ALBA Fee

On *Calyptranthes*, Ubero; also, not typical, on *Torrubia*, Sardinera.

The collection also contains a sterile plant near *Omphalaria Wrightii* Tuck., from wet, sunny soil between Sardinera and

Ubero, a sterile species of the *Dermatocarpaceae* growing on limestone at Ubero, and three other sterile and undeterminable specimens.

BASIDIOMYCETES

(Determined by Dr. W. A. Murrill)

LENTINUS CRINITUS (L.) Fries

On dead wood, Ubero: Porto Rico; Bahamas.

SCHIZOPHYLLUM ALNEUM (L.) Schroet.

Frequent on dead wood: Porto Rico; Bahamas.

DAEDALEA AMANITOIDES Beauv.

On dead wood, Ubero: Porto Rico; Bahamas.

INONOTUS CORROSUS Murr.

On dead wood, Sardinera: Porto Rico; Bahamas.

PYROPOLYPORUS DEPENDENS Murr.

On dead wood: Porto Rico; Bahamas.

POGONOMYCES HYDNOIDES (Sw.) Murr.

On dead wood: Porto Rico; Bahamas.

PYCNOPORUS SANGUINEUS (L.) Murr.

Frequent on dead wood at base of escarpment: Porto Rico; Bahamas.

CORIOLOPSIS RIGIDA (Berk. & Mont.) Murr.

On dead wood, Sardinera: Porto Rico; Bahamas.

CORIOLUS PINSITUS (Fries) Pat.

On dead wood: Porto Rico; Bahamas.

XYLARIA

On dead log, Ubero.

UREDINALES

(Determined by Professor J. C. Arthur)

COLEOSPORIUM PLUMIERAE Pat.

On *Plumiera obtusa*.

KUEHNEOLA GOSSYPHII (Lagerh.) Arth.

On *Gossypium barbadense*.

PUCCINIA CENCHRI Dietr. & Holw.

On *Cenchrus*.

PUCCINIA CRASSIPES B. & C.

On *Ipomoea triloba* L.

PUCCINIA EUPHORBIAE P. Henn.

On *Aklenea petiolaris* (Sims) Millsp.

PUCCINIA INFLATA Arth.

On *Stigmaphyllon lingulatum* (Poir.) Small

PUCCINIA LATERITIA B. & C.

On *Ernodea littoralis* Sw.

- PUCCINIA URBANIANA P. Henn.
 On *Valerianodes strigosa* (Vahl) Kuntze
- UREDIO BIOCELLATA Arth.
 On *Pluchea purpurascens* (Sw.) Kuntze
- UREDIO CAMELIAE Mayor.
 On *Chaetochloa setosa*.

Many parasitic fungi collected by Professor Stevens have not yet been determined.

ALGA

(Determined by Professor N. Wille)

- SCYTONEMA OCELLATUM Lyngb.
 Flat limestone plateau, Ubero.

RECAPITULATION

Species indicated in the foregoing list.....	292
Deduct thallophytes (distribution little known).....	47
	<hr/> 245
Deduct undetermined and doubtfully determined species.....	12
	<hr/> 233
Deduct certainly introduced species.....	8
	<hr/> 225
Deduct endemic species.....	4
	<hr/> 221
In common with Porto Rico.....	211
" " " Hispaniola	185
" " " Bahamas	155
" " " Curacao	87

SPECIES OTHER THAN ENDEMIC ONES AND THALLOPHYTES NOT
 KNOWN ON PORTO RICO (INCLUDING DESECHEO, CULEBRA
 AND VIEQUES)

- Cenchropsis myosuriodes: Bahamas; Cuba.
 Domingoa hymenodes: Hispaniola; Cuba.
 Caesalpinia domingensis: Hispaniola.
 Guilandina melanosperma: St. Croix.
 Dodonaea Ehrenbergii: Bahamas; Hispaniola; Cuba.

Sarcomphalus Taylora: Bahamas.

Plumiera obtusa: Hispaniola; Bahamas; Cuba.

Brachiolejeunea bahamensis: Florida; Bahamas.

Hyophila guadelupensis: Guadeloupe; Montserrat.

Bryum subdecurrens: St. Thomas.

EXPLANATION OF PLATE

PLATE 1

- Fig. 1. Escarpment, Mona Island, showing openings of caves.
Fig. 2. Part of Mona Island from the ocean, showing escarpments and plateau.



Fig. 1



Fig. 2

BRITTON—VEGETATION OF MONA ISLAND

EXPLANATION OF PLATE

PLATE 2

Fig. 1. Escarpment and tables, Mona Island.

Fig. 2. Coastal thicket, Mona Island.



Fig. 1



Fig. 2

BRITTON—VEGETATION OF MONA ISLAND

THE FLORA OF NORWAY AND ITS IMMIGRATION

N. WILLE

Professor at the Christiania University

The phytogeographical investigations in a country may be carried on in the following three main directions:

Floristic phytogeography, or an investigation into the geographical distribution of the plant species. The result of this work should be charts of the distribution in the country of the various species. In a country with such varied conditions of life as Norway, this is a very comprehensive and very arduous task, requiring an infinitude of detailed investigations in all parts of the country.

Ecological phytogeography, which endeavors to find out how and why the different species of plants in various places and under various conditions of life come together in plant-communities. This branch of science, which was founded by Professor E. Warming, must be based upon phytoanatomy and phytophysiology, as the connection between the organization of the vegetable species and their external conditions of life must be investigated. Investigations such as these may yield interesting results in all countries, and are most easily carried on where the conditions of life are uniform over wide areas; but in a country like Norway, with its varied conditions, they present very great difficulties.

Historical phytogeography has for its aim the investigation of the changes that in the course of time have taken place in the vegetation of a country—to find out, for instance, when and whence important species have immigrated, how quickly they have spread, why others, that had formerly been more widely distributed, had a more restricted distribution in a later period, etc., etc.

With regard to this last branch of science, the Scandinavian countries, Denmark, Finland, Norway, and Sweden, present peculiarly favorable conditions; for there is no doubt that these countries were formerly buried under a continu-

ous covering of ice, which destroyed all vegetation except perhaps the most hardy. All other species of plants have immigrated subsequently from the neighboring countries, which were not covered with ice during the Glacial Epoch, and could therefore afford a dwelling-place for a more or less abundant flora.

In the following pages I shall endeavor to give an account of the results at which historical phytogeography may be said to have arrived as far as Norway is concerned.

SURVEY OF THE DISTRIBUTION OF THE NORWEGIAN FLORA

It will first be necessary, however, to give a general account of the most important points regarding the composition and distribution of the Norwegian flora throughout the country. I shall here consider only the vascular plants (about 1,500 species), however, as the distribution of the lower plants is not sufficiently known to enable us to draw definite conclusions.

The area of Norway is about 125,000 square miles, stretching from latitude $57^{\circ} 58' 43''$ north to latitude $71^{\circ} 10' 20''$ north. The conditions for plant life will thus be very different in the southern and northern parts of the country. But in addition to this, there is a great difference between the climate in the east and that in the west of southern Norway. In the valleys of the East Country, there is a very pronounced inland climate, with hot summers and a winter temperature that falls below -40°C. , while on the west coast region there is a low summer temperature, but a mean January temperature of sometimes more than 2°C.

The most important condition affecting the distribution of plants in Norway is the temperature. In this connection we shall in the first place speak of the lowest winter temperature that the plants can survive. J. Holmboe ('13) has shown that the distribution of *Ilex aquifolium* in Norway coincides closely with the January isotherm for 0°C. Herbaceous plants which die down in the winter may of course be independent of the lowest winter temperature, as they are covered with snow; but they are not entirely independent of

the spring and autumn temperature. Plants are also in a great measure dependent on the height of the temperature in the period of vegetation, which, in Norway, comprises in the main the four months, June, July, August, and September.

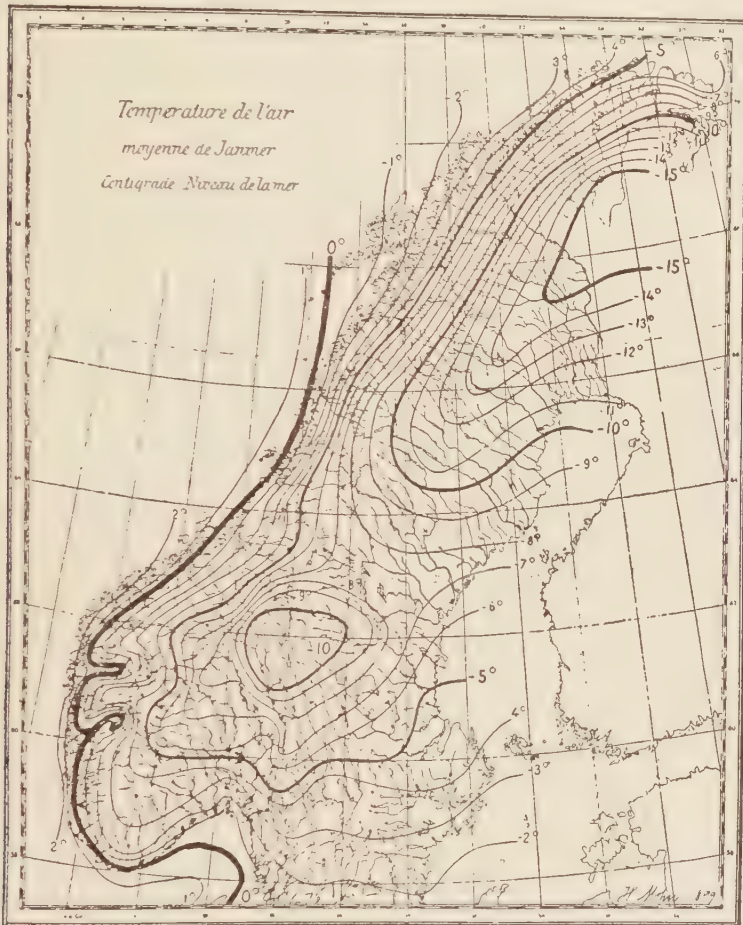


Fig. 1. Isotherms for January.

In this way, the conditions prevailing in Norway are very varied, the July isotherm for Christiania being $17^{\circ}\text{C}.$, while for the west coast it is only from 12 to $14^{\circ}\text{C}.$

A. Helland ('12) has calculated that where the mean summer temperature in Norway is less than $13^{\circ}\text{C}.$, the fruit

trees yield nothing worth mentioning; and where it is less than 11°C. , the cultivation of grain is uncertain. The minimum limits of the necessary mean summer heat for the following wild Norwegian trees and shrubs appears to be as

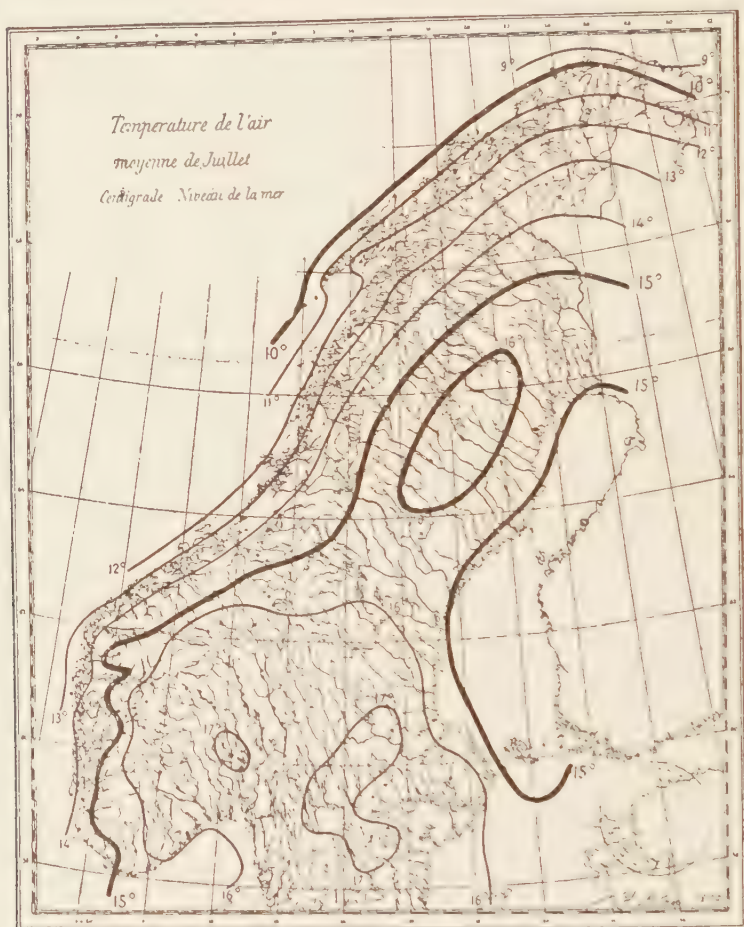


Fig. 2. Isotherms for July.

follows: for *Fagus sylvatica*, 13.4°C. ; *Quercus pedunculata*, 12.6°C. ; *Corylus Avellana*, *Acer platanoides*, and *Tilia cordata*, 12.5°C. ; *Alnus glutinosa* and *Fraxinus excelsior*, 12.4°C. ; *Sorbus Aria* and *Ulmus montana*, 11.2°C. ; *Picea excelsa* and *Pinus sylvestris*, 8.4°C. ; *Alnus incana*, *Prunus Padus*,

and *Sorbus Aucuparia*, 7.7°C.; *Populus tremula*, 7.6°C.; *Betula odorata*, 7.5°C.; *Juniperus communis* var. *nana*, 5.3°C.; and *Betula nana*, 4.3°C.

As the mean temperature of summer decreases with increasing height above sea-level very nearly 0.6°C. per 330 feet, the distribution of plants is greatly influenced by the circumstance that Norway is a mountainous country, its highest mountain, Galdhøpiggen, being 8,095 feet in height, and thus within the region of perpetual snow. But a peculiarity of the Norwegian mountains is that they form broad (as much as sixty-two miles broad), undulating mountain plateaus, which are intersected by deep or shallow valleys, where there are narrow lakes or small rivers. The edge of these mountain plateaus, in the south of Norway, lies at a height of from 2,950 to 3,280 feet above the sea, so that *Picea excelsa* and *Pinus sylvestris* disappear slightly below this height, the edge of the plateaus and the lowest valleys that intersect them being covered with *Betula odorata*. The great mass of the mountain plateaus, which rise above the birch-limit, is thus treeless.

It has been calculated that there are 26,333 square miles of forest land in Norway, of which 73 per cent consists of *Picea excelsa* and *Pinus sylvestris*, while the remaining 27 per cent is mainly *Betula odorata* with a little *Betula verrucosa*, *Quercus pedunculata*, and *Q. sessiliflora*, and a very little *Fagus sylvatica* in the south.

The vegetation limits are lower not only toward the north, as one would expect, but also toward the west, as they are lower near the sea than inland. This will be seen from the following height-limits in feet:

	Snow-line ft.	Birch-limit ft.	Pine-limit ft.
Gausta in Telemarken (south of Norway)	3450	3024-3113
Vos (west of Norway)	3936	3359	1994
Snehaetta, in the Dovre Mountains (central Norway)	5375	3464	2880
Rödö in Helgeland (just within the Arctic Circle)	3280	777
Alten in Finmark (70° N. Lat.).	3516	1476	777-1023

The distribution northward and height above sea-level of the various vegetable species, will be dependent mainly upon the temperature during the summer months.

The rainfall, which in various other countries plays so important a part as a factor in vegetation, is of less import-

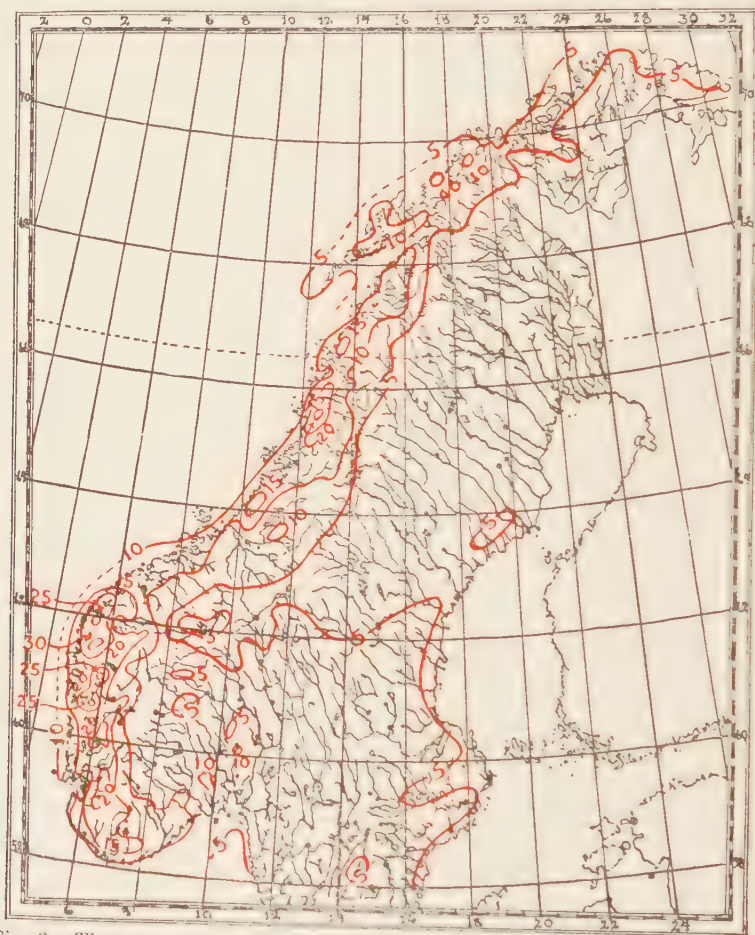


Fig. 3. The annual rainfall in Norway (in centimeters).—After M. Mohn.

ance in Norway, as even on the Dovre Mountains, where the rainfall is smallest (about 300 mm. per annum), there is sufficient rain to occasion, on account of the inconsiderable evaporation, swamps and peat-bogs, where even entirely hydrophilous communities thrive.

It was formerly supposed that the largest rainfall was on the outermost islands off the west coast of Norway, and that this was the cause of the Atlantic vegetation that is found there, with such characteristic plants as *Hymenophyllum peltatum*, *Erica cinerea*, *Scilla verna*, *Vicia Orobus*, etc. But more recent investigations have shown that the rainfall is greater a little way in from the coast, where the mountains begin. In Hovlandsdal, near the Sogne Fjord, a mean rainfall has been observed of 3,178 mm., and at Skaanevik, near the Folgefon, 2,945 mm., whereas the outermost islands off Bergen show a rainfall of only 1,300 mm., and off Florö of 1,900 mm. It is, therefore, clear that the occurrence of the above-mentioned Atlantic plants on the outermost islands is due not to a larger rainfall, but to a milder winter temperature.

There are, of course, species of plants that cannot thrive in the great humidity of the West Coast; but as there are also localities with comparatively dry soil, it may be rather the low summer temperature than the large rainfall that prevents them from thriving.

The importance of the soil for vegetable growth appears to depend, in Norway, mainly upon whether the soil is rich, or deficient, in lime. In addition to its chemical influence, a calcareous subsoil, especially when consisting of calcareous slate or limestone, is of consequence from the fact that it forms a warm soil. In Norway, therefore, most of the southern species are found only in the limestone country surrounding the Skien Fjord and the upper part of the Kristiania Fjord.

The terrestrial plants of Norway may be divided into five zones, according to the ability of the plants to ascend the mountains and extend northward in their growth, that is to say, according to their dependence on the mean temperature of the summer. These zones are here indicated by the upper limit of a characteristic species of plant.

I. THE QUERCUS PEDUNCULATA ZONE

In the east of Norway this tree is found as far as Lake Mjösen (60° 45' N.), and in the west up to Nordmøre (62°

55'); but it is nowhere known to have reached a greater height above sea-level than 1,722 feet.

The oak can stand a winter temperature as low as -33.8° C., but requires a mean summer temperature of 12.6° C. It is now comparatively rare, and seems to be decreasing. It occurs in large quantities only on the Silurian and along the lower parts of the coast.

A number of deciduous trees that are susceptible to cold have about the same distribution as the oak, both in height and in northward extension. These are: *Acer platanoides*, *Alnus glutinosa*, *Betula verrucosa*, *Crataegus Oxyacantha*, *Fraxinus excelsior*, *Prunus avium*, *P. insititia*, *Pyrus Malus*, *Sorbus Aria*, *S. fennica*, *Taxus baccata*, and *Tilia cordata*. There are also a number of species of cryptogams. It may on the whole be said that the zone here designated the Oak Zone is that of Norway's most abundant flora.

Within the Oak Zone, large districts may in their turn be marked off that possess a characteristic flora, the occurrence of which is especially conditioned by circumstances of temperature and soil.

1. *The Region of the Silurian Flora.*—This is developed in an especially characteristic manner on the calcareous slate along the Langesund Fjord, the west side of the Kristiania Fjord, in Ringerike and Hadeland, and around Lake Mjøsen. In some of these districts it is fairly cold in the winter, but very hot in the summer;¹ and as the soil is calcareous and warm, a xerophilous steppe-flora, with its characteristic *Labiatae*, *Boragineae*, and *Centaurea* species, and thistles, such as *Carlina vulgaris*, *Carduus acanthoides*, etc.—species which also occur in the steppe-regions of South Russia, can thrive well on southern slopes.

For the rest, the flora is rich in characteristic species, e.g., *Artemisia campestris*, *Brachypodium pinnatum*, *Carex prae-cox*, *Cephalanthera rubra*, *Cirsium acaule*, *Fragaria collina*, *Labianotis montana*, *Ononis campestris*, *Phleum phalaroides*,

¹ In Kristiania, the 30-years' average minimum atmospheric temperature for the month of January is -16.5° C., and the average maximum for the month of June $+28.9^{\circ}$ C.

Spiraea Filipendula, *Thymus Chamaedrys*, *Trifolium montanum*, *Veronica spicata*, etc.

Where the soil is deep and not too dry, the above-mentioned deciduous trees that are susceptible to cold form forests or copses, intermingled with *Corylus Avellana*, *Prunus spinosa*, species of *Rosa* and *Rubus*, and a luxuriant ground vegetation, among which are several orchids.

A few of these trees and the more hardy species of the Silurian flora, such as *Origanum vulgare* and others, may, like an advance-guard, overstep the boundaries of the Silurian regions, but then they generally occur in warm localities, in talus at the foot of cliffs, or in steep slopes that face southward, even high up the sides of the valleys, or in the upper parts of the West Country fjords.

But the number of species diminishes with increasing distance from the lowland Silurian regions, and there are only a few species that have advanced as far as north of the Dovre Mountains.

2. *The Region of Fagus sylvatica*.—This region is situated along the southeast coast of Norway, from the Swedish border to Grimstad, where it extends as far north as Holmestrand. There is a small beech-wood a little to the north of Bergen, but this is a solitary instance, and has nothing to do with the real distribution area of the beech.

The beech is purely a lowland plant, as there is only one place in which it goes to a height of 886 feet above the sea, its usual height being not more than 525 feet. When cultivated, it can grow almost as far north as *Quercus pedunculata*, but prefers a rather higher summer temperature (13.4°C.) and thrives best on comparatively warm gravel banks.

The beech is one of those plants which has recently appeared to spread to new regions; and there is no doubt that it has not yet nearly reached the limits of distribution to which it will little by little attain, especially along the low land of the south coast. This is due to the fact that it must have immigrated in fairly recent times.

The following plants may also be mentioned as occurring chiefly in the region of the beech: *Cladium Mariscus*, *Coron-*

illa Emerus, *Epilobium obscurum*, *Laserpitium latifolium*, *Ligustrum vulgare*, *Luzula nemorosa*, *Melampyrum cristatum*, *Rubus corylifolius*, *R. Lindebergii*, *Selinum carvifolium*, *Sium latifolium*, *Viscum album*, *Vicia cassubica*, *V. lathyroides*, etc. A few of these have a rather larger distribution than the beech has at present; others, which must have immigrated recently, are found only within quite a small area.

The region for the cultivation of wheat in Norway coincides in the main with that of the beech, but extends a little farther, namely westward as far as Mandal, and to a height of 1,246 feet above sea-level.

3. *The Region of Ilex Aquifolium*.—This region is situated a little to the west of that of the beech, and does not have a lower mean temperature for January than 1°C. It extends from Arendal to Christianssund (63° 7' N. Lat.), but does not include the outermost islands on the west coast.

A large number of vegetable species occur in this region. As especially characteristic may be mentioned *Aeropsis prae-cox*, *Asplenium Adiantum nigrum*, *Cardamine hirsuta*, *Centaurea decipiens*, *C. nigra*, *C. pseudophrygia*, *Cerastium tetrandrum*, *Chrysosplenium oppositifolium*, *Circaea lutetiana*, *Conopodium denudatum*, *Corydalis claviculata*, *Cynosurus cristatus*, *Digitalis purpurea*, *Drosera intermedia*, *Gentiana Pneumonanthe*, *Geranium columbinum*, *Hedera Helix*, *Hieracium australe*, *Hydrocotyle vulgaris*, *Hypericum pulchrum*, *Hypochaeris radicata*, *Juncus squarrosus*, *Leontodon hispidus*, *Luzula sylvatica*, *Lysimachia nemorum*, *Meum athamanticum*, *Quercus sessiliflora*, *Pilularia globulifera*, *Polygala depressum*, *Primula acaulis*, *Rosa pimpinellifolia*, *Rumex obtusifolius*, *Sagina subulata*, *Scirpus setaceus*, *Sedum anglicum*, *Senecio Jacobaea*, *Stellaria Holostea*, *Teesdalia nudicaulis*, *Triticum acutum*, *T. junceum*, and *Weingartneria canescens*.

A few of these species, however, can bear a January isotherm that lies a little lower than 1°C. These species, among which are *Hedera Helix* and *Quercus sessiliflora*, occur, therefore, also in the beech region in the southeast of Norway, but have their chief distribution in the *Ilex* Region, and must therefore be assigned to that region.

4. *The Region of the West-European Coast Flora.*—This includes the outermost islands in the province of Bergen. The characteristic feature of the climatic conditions here, as we have already stated, is not the large rainfall, for this is in reality smaller than in certain parts of the Ilex Region; but it is the extremely mild winter temperature, and a comparatively low summer temperature.

For purposes of comparison we will here give the mean minima for February and the mean maxima for July, for Kristiania, which forms a center for the Silurian flora, Larvik, the center of the beech region, Mandal of the holly, and Utsire of the West-European coast flora.

	Mean minimum temperature for February	Mean maximum temperature for July
Kristiania	15.5° C.	28.8° C.
Larvik	14.5° C.	25.8° C.
Mandal	11.3° C.	24.8° C.
Utsire	5.7° C.	19.9° C.

On these outermost islands in the province of Bergen, the mean temperature for January is 2°C.

Among the plant species that are especially characteristic of this region may be mentioned *Asplenium marinum*, *Erica cinerea*, *Hymenophyllum peltatum*, *Scilla verna*, and *Vicia Orobus*. These species are found in England, and some of them southward along the shore of the Atlantic.

II. THE PINUS SYLVESTRIS ZONE

In the east of Norway *Pinus sylvestris* goes right down to the sea, and occurs in many places in the Oak Zone; but in speaking here of a special zone for *Pinus sylvestris*, we refer to the great continuous forests of *Pinus sylvestris* and *Picea excelsa*, which cover wide tracts of country from the upper limit of the Oak Zone to a height of 3,116 feet in the south of Norway, 1,640 in the central part, and 623 in the north. *Pinus sylvestris* avoids the sea, and is therefore absent from the outermost belt of islands; but inland it forms, either alone or together with *Picea excelsa*, a more or less continuous region of distribution below the above-stated height-limits up to latitude 70°N.

Picea excelsa, which immigrated much later than *Pinus sylvestris*, supplants the latter in favorable localities in the east of Norway; but in the west its field of distribution is very small, and extends only to latitude 69°N. Farther north, in the interior of Finmark, small spruce forests do indeed occur, but they are formed of *Picea obovata*.

The forests that are formed of *Pinus sylvestris* are light, but as they often grow upon dry, poor soil, they are poorly furnished with vegetable species. There may occur scattered specimens of *Betula odorata*, *Alnus incana*, *Juniperus communis*, *Sorbus Aucuparia*, and *Populus tremula*, and then a poor ground vegetation of mosses (e.g., *Polytrichum juniperinum*), and lichens (e.g., *Cladonia rangiferina*, *Cetraria islandica*, and *Peltigera*), among which grow some easily contented higher plants, especially *Aira flexuosa*, *Arctostaphylos officinalis*, *Calluna vulgaris*, *Empetrum nigrum*, *Festuca ovina*, *Luzula pilosa*, *Melampyrum sylvaticum*, *Pteris aquilina*, *Trientalis europaea*, *Vaccinium Myrtillus*, *V. uliginosum*, and *V. Vitis-Idaea*.

Where this forest, from some cause or other, has been destroyed, extensive heath-lands are often formed, consisting chiefly of *Calluna vulgaris*, among which occur *Empetrum nigrum* and species of *Vaccinium*, as also *Antennaria dioica*, *Aira flexuosa*, *Campanula rotundifolia*, *Festuca ovina*, *Nardus stricta*, and others.

Picea excelsa forms forests on more fertile soil; but as they are very dense and dark, other trees have difficulty in forcing an entrance, and even the ground vegetation is as a rule very poor, owing to the want of light. A thick carpet of mosses (especially *Hylocomium splendens*) covers the ground, and the only plants that thrive are fungi, *Polystichum spinulosum* and some other ferns, *Linnæa borealis*, *Milium effusum*, *Oxalis Acetosella*, *Pyrola uniflora*, and others.

Where the forests of *Picea* are less dense, or where *Pinus sylvestris* grows upon a more fertile soil, these conifers may be mingled with various deciduous trees, and in the lower districts even with less hardy deciduous trees, which otherwise belong to the Oak Zone. The ground vegetation in such

places is also much more abundant, and the ordinary lowland flora may be found fairly well represented.

Almost all cultivated land in Norway lies in the Oak and Pine Zones. Rye and oats ripen up to latitude 69°N. , barley even up to 70°N. —in the south it can be grown up to a height of 2,066 feet above the sea. The potato is cultivated rather farther north and a little higher above sea-level than barley. Side by side with the growing of grain is that of forage plants, of which the most important species are *Trifolium pratense* and *Phleum pratense*.

III. THE BETULA ODORATA ZONE

Betula odorata also occurs in the lowlands, and extends farther toward the sea than *Pinus sylvestris*, but by its zone, as here defined, is meant the region above the height limit of *Pinus sylvestris* upon the mountains and north of its distribution. In the very south of Norway, *Betula odorata* goes up to about 3,600 feet above the sea, and northward as far as latitude $71^{\circ} 10' \text{N.}$ Thus beyond the Birch Zone there is only the northeastern part of Finmark and the highest mountain regions.

In the south of Norway the great proportion of the so-called "saeters" lies in the Birch Zone, as this tree generally occupies the margin of the mountain wastes, and fills the little valleys that intersect them with a short-stemmed forest of *Betula odorata* subsp. *alpigena*.

Side by side with this mountain form of birch, there may also grow *Alnus incana*, *Populus tremula*, *Prunus Padus* and *Sorbus Aucuparia*. The ground vegetation will be somewhat variable according to the degree of moisture in the soil.

On dry gravelly slopes, especially if they face the south, the following species of higher plants are generally found in addition to a few species of lichens, such as *Cetraria islandica*, *Stereocaulon*, etc.: *Arctostaphylos officinalis*, *Agrostis vulgaris*, *Aira flexuosa*, *Alchemilla alpina*, *A. vulgaris* var. *pubescens*, *Antennaria dioica*, *Anthoxanthum odoratum*, *Astragalus alpinus*, *Botrychium Lunaria*, *Betula nana*, *Calluna vulgaris*, some species of *Carex*, *Empetrum nigrum*

Euphrasia officinalis, *Festuca ovina*, *Gnaphalium norvegicum*, *Juniperus communis*, *Lotus corniculatus*, *Luzula campestris*, *L. pilosa*, *Maianthemum bifolium*, *Melampyrum sylvaticum*, *Nardus stricta*, *Pedicularis Oederi*, *Peristylis viridis*, *Phleum alpinum*, *Poa alpina*, *Pyrola minor*, *Rhinanthus minor*, *Solidago Virgaurea*, *Trientalis europaea*, *Vaccinium Myrtillus*, *V. uliginosum*, *V. Vitis-Idaea*, and *Vicia Cracca*.

Where the soil is deeper and damper, and along streams and in shady places, *Salix glauca*, *S. hastata*, *S. lanata*, *S. lapponum*, *S. Myrsinites* and their hybrids make their appearance. The vegetation here is more luxuriant, as in addition to most of the above-named, the following species are found: *Aconitum septentrionale*, *Agrostis rubra*, *Alchemilla vulgaris* var. *alpestris*, *Aira alpina*, *A. caespitosa*, *Bartschia alpina*, species of *Carex*, *Equisetum hiemale*, *Geranium sylvaticum*, *Gymnadenia conopea*, *Montia fontana*, *Mulgedium alpinum*, *Myosotis sylvatica*, *Orchis maculata*, *Polygonum viviparum*, *Pinguicula vulgaris*, *Polemonium caeruleum*, *Ranunculus platanifolius*, *Rumex Acetosa*, *Saussurea alpina*, *Selaginella spinulosa*, *Soyera paludosa*, *Spiraea Ulmaria*, *Viola biflora*, and others. Many of these species occur right down to sea-level, some also higher up in the next zone; but as they are always found in the Birch Zone and have their most abundant development there, it is best to refer them to that zone.

IV. THE ZONE OF DWARF WILLOWS

This zone occupies the northeast part of the Varanger peninsula in Finmark and the mountains above the birch limit, up to a height which, in the southernmost point, may be put at 4,133 feet above the sea. It is thus only the tops of the highest mountains which rise like islands above this zone. The mean summer temperature here will be from 8.5 to 4.3 °C., according to the height and situation in higher latitudes. The composition of the vegetation varies greatly according to the moisture conditions of the soil, which in their turn to some extent depend on exposure to the sun, south slopes being dry, north slopes damp.

On the drier tracts there are low copses of *Betula nana* and *Juniperus nana*, with a ground vegetation of mosses and lichens and a poor selection of mountain plants, such as *Antennaria alpina*, *Arctostaphylos alpina*, *Azalea procumbens*, *Carex rigida*, *Hieracium alpinum*, *Juncus trifidus*, *Erigeron alpinus*, *E. uniflorus*, *Festuca ovina*, *Gnaphalium supinum*, *Luzula arcuata*, *Luzula nivalis*, *L. spicata*, *Lycopodium alpinum*, *L. Selago*, *Nardus stricta*, *Pedicularis lapponica*, *Polygonum viviparum*, *Rhodiola rosea*, *Salix herbacea*, *S. reticulata*, *Trientalis europaea*, *Vaccinium Myrtillus*, *V. uliginosum*, *V. Vitis-Idaea*, *Viscaria alpina*, and others.

Where the soil is very poor and the climate during the vegetation period very dry, as on the mountain moorlands in the east of Norway—'round the lake Faemundsoe, and between the valleys Oesterdal and Gudbrandsdal—there occur great lichen-covered heaths consisting of *Cladonia rangiferina*, *Cetraria nivalis*, *C. cucullata*, *Alectoria divergens*, and *A. nigricans*, which give a grayish white appearance to the mountains. Among the masses of lichens there are found only a few very easily satisfied mountain plants such as *Festuca ovina*, *Nardus stricta*, *Solidago Virgaurea*, etc.

Where, on the other hand, the soil abounds in lime, and the conditions otherwise are favorable, as in certain places on the Hardanger Plateau in the south, Lom and Dovre in the center, and several places in the north of Norway, rare mountain plants occur, such as *Alsine biflora*, *A. hirta*, *Dryas octopetala*, *Primula scotica*, *P. stricta*, *Oxytropis lapponica*, *Papaver radiculatum*, *Rhododendron lapponicum*, *Salix polaris*, *Veronica saxatilis*, etc.

If the soil, on the contrary, is deep and damp, as in morasses and along streams, or where water trickles down the sides of mountains, there is quite a different and more abundant vegetation, consisting of mosses with thickets of *Salix glauca*, *S. lanata*, *S. lapponum*, and *S. Myrsinites*, often with an undergrowth of *Aira alpina*, *Andromeda hypnoides*, *Cardamine bellidifolia*, *Cerastium trigynum*, *Eriophorum capitatum*, *E. vaginatum*, *Juncus biglumis*, *J. castaneus*, *J. triglumis*, *Koenigia islandica*, *Oxyria digyna*, *Petasites frigida*,

Ranunculus glacialis, *R. nivalis*, *R. pygmaeus*, *Saxifraga aizoides*, *S. caespitosa*, *S. rivularis*, *S. stellaris*, *Silene acaulis*, *Tofieldia borealis*, *Vahlodea purpurea*, *Veronica alpina*, etc.

V. THE LICHEN ZONE

This embraces the often stony tracts above the preceding zone, i.e., the highest mountain tops and the ground from which they rise.

Rocks and stones are here covered with the blackish yellow *Lecidea geographica* and other lichens. Where there is a little soil, some hardy mosses grow, and under favorable conditions a very few species of higher plants.

I may mention, as an illustration, that in 1877, when visiting the mountain Haarteigen (5,546 feet) in Hardanger, i.e., in the south of Norway, I noted the following higher plants upon the comparatively flat top of the mountain: *Carex rigida*, *Luzula arcuata*, *L. spicata*, *Lycopodium Selago*, *Poa alpina*, *Polygonum viviparum*, *Ranunculus glacialis*, and *Rhodiola rosea*.

As already repeatedly stated, all plant species are not strictly confined to the zone under which they are mentioned as especially characteristic factors. It is very general for species somewhat to overstep the boundaries of their true zone, either upward or downward. Certain species are even found in all zones from the sea to the snow, since they have a remarkable ability of adapting themselves to all kinds of soil and to all kinds of climatic conditions. As instances of such species we may mention *Calluna vulgaris*, *Empetrum nigrum*, *Eriophorum vaginatum*, *Festuca ovina*, *Nardus stricta*, *Polygonum viviparum*, and the species of *Vaccinium*.

Another circumstance is that typical mountain plants are sometimes found in the lowlands right down to the sea, e.g., in Jaederen, *Alchemilla alpina*, *Arctostaphylos alpina*, *Bartschia alpina*, *Saxifraga aizoides*, and *Selaginella spinulosa*. *Betula nana* occurs in the southeast of Norway down to fifty feet above the sea, and *Dryas octopetala* occurs at Lange-sund and at Varaldsö in Hardanger at sea-level. These occurrences were formerly often explained as relics of a previ-

ous age with a colder climate, but I do not think we need have recourse to such an explanation. In all the steep-sided valleys, typical mountain plants spread downward along streams and rivers, and often appear far below their real habitat. Whether they will remain there depends only upon their ability to compete with lowland plants and to withstand the night frosts in the spring after the snow has melted.

I assume, therefore, that the occurrence of the above-mentioned mountain plants in the lowlands is due to a chance carrying of seed to places that were favorable to the welfare of the species, e.g., limestone at Langesund and Varaldsö for *Dryas octopetala*, a peat-bog for *Betula nana*, and so forth.

THE IMMIGRATION OF THE NORWEGIAN FLORA

Geologists have long been agreed that Scandinavia and great parts of adjacent lands have once been covered with one entire ice-cap, as the interior of Greenland is at the present time. By degrees the view obtained that there have really been two such glacial epochs, separated by an intermediate warm period, in which the conditions probably more or less resembled those of the present day.

During the first, called the Great Glacial Epoch, the ice-cap extended as far as central Germany, over almost the whole of England, over the whole of Finland, and over a great part of northern Russia. It follows that under such conditions, all, or almost all, vegetation must have disappeared from the Scandinavian peninsula, from Norway and Sweden. I am inclined to believe that in places in Norway, the tops of high mountains rose above the ice-covering, and that a very few species of plants may have survived there; but this is a matter of no interest in the question upon which I shall now endeavor to throw light, namely, the immigration of the flora of Norway after the Last Glacial Period.

This was of considerably smaller extent. On the south the ice reached only as far as Mecklenburg, and the ice-boundary then ran obliquely northward up through Jutland in Denmark, of which, therefore, only a part was entirely covered with ice. There can be no doubt that the whole of

Sweden was covered by this ice-cap, but as regards Norway, the conditions are still a matter of dispute. Some geologists maintain that the ice went right out into the sea on all sides; others assume that in some parts there was an iceless coast-region, where only here and there great glaciers ran out into the sea.

The great majority of the species in the Norwegian flora must, however, have immigrated after the last Glacial Period; but with regard to their immigration and the conditions under which it took place, various theories have been advanced.

The first to take up this question, especially with regard to Sweden, was F. W. Areschoug ('66), who, in 1866, maintained that the present vegetation of Scandinavia was made up of at least three elements of different period and origin, namely:

(1) An arctic vegetation, which immigrated from the east during the latter part of the Glacial Period, and, from its origin, may be called the *North Siberian Flora*;

(2) A northeastern and eastern vegetation, which came into Europe from Siberia after the Glacial Period, but before the immigration of the beech. From its origin, it may be called the *Altai Flora*;

(3) A southeastern and southern vegetation, which came simultaneously with the beech, partly from the Caucasus and the countries 'round the Caspian and Black Seas, partly from the countries of the Mediterranean. This may be called the *Caucasian and Mediterranean Flora*.

Areschoug also pointed out that a number of arctic species in the north German and south Swedish lowlands must be regarded as relics of the vegetation of the high north, which, after the melting of the ice-cap, withdrew toward the north or up into the mountains.

This view received strong support in the discovery by A. G. Nathorst ('71) in 1870, in the fresh-water clays of the south of Sweden, of remains of typical arctic plants which do not grow there now, but only very much farther north, namely, *Betula nana*, *Dryas octopetala*, *Salix herbacea*, *S. polaris*, and *S. reticulata*.

In 1875, Axel Blytt ('76) first brought forward his well-known theory on the immigration of the flora of Norway during alternate wet and dry periods. According to Blytt's theory, the wild plants of Norway should be arranged in the following six groups: (1) the *arctic* (the mountain flora); (2) the *subarctic* (the vegetation of mountain and wooded slopes), which is more frequent in the arctic than in the more southern, lower regions; (3) the *boreal* (the vegetation of the rocky slopes covered with foliage trees), which has its widest distribution in the low land, but not the coast districts; (4) the *Atlantic* (Bergen coast vegetation), with distribution in the coast district, especially between Stavanger and Kristianssund; (5) the *sub-boreal*, which occurs in the southeast of the country, especially 'round the Kristiania Fjord; and (6) the *sub-Atlantic* (Kristianssand coast vegetation), which has its widest distribution in the coast district between Kragerö and Stavanger.

The arctic, boreal, and sub-boreal species of plants are warmth-loving, continental plants, while the subarctic, Atlantic, and sub-Atlantic keep chiefly to the coast districts and are insular in character. The former have immigrated during dry periods, the latter during damp periods, in the order in which they have been placed. Blytt assumed that within the period of history it is scarcely probable that any very great changes have taken place in climate or vegetation, and that the present is a dry period.

Blytt ('83) subsequently maintained that these changes of climate were due to cosmic causes, namely alterations in the eccentricity of the earth's orbit and alternate changes in the earth's position with regard to the sun, occupying periods of about 21,000 years. By the aid of this hypothesis he calculated the period from the conclusion of the Glacial Epoch down to the present time to be between 80,000 and 90,000 years. The damp and dry periods were thus of equal duration, namely 10,500 years.

As Blytt moreover started with the assumption that the plants could advance only step by step in their migrations, and could not be transferred direct from Denmark or England

to Norway, he supposed that the six different flora-elements had immigrated from the south through Sweden to the places in which they are now found, but during the subsequent change of climate had died out in the intermediate regions, in which they do not grow now.

Since then, Gunnar Andersson ('96, '06) has discussed this question with special reference to Sweden. He builds more particularly upon paleontological studies of the plants preserved in peat-bogs. He assumes that the climate, after the melting of the ice, continued to grow warmer until—since *Corylus Avellana*, according to fossil occurrences, had a far more northerly distribution area than at the present time—it showed a mean temperature in August that was about 2.5° C. higher than at the present time. The temperature has, therefore, fallen to that of the present day.

Gunnar Andersson designates the various periods after the Glacial Epoch according to the most characteristic plant, and assumes that the immigration has taken place in the following order:

(1) The *Dryas Flora* includes certain arctic species, e.g., *Dryas octopetala*, *Salix herbacea*, *S. polaris*, *S. reticulata*, *Oxyria digyna*, *Arctostaphylos alpina*, and others, which are supposed to have migrated into Sweden when the melting of the ice had begun, and followed this northward. The most northerly place, however, where these arctic plants are found in Sweden is in West Gothland, in about the latitude of Gothenburg. They have not been found, from this period, farther north.

(2) The *Betula odorata Flora* is more subalpine. With it came also *Salix aurita*, *S. caprea*, and *S. cinerea*, etc.

(3) The *Pinus sylvestris Flora* immigrated during a somewhat warmer period, which continued to grow warmer. In the lower, and thus older, part of the Pine Zone are found *Prunus Padus*, *Rubus idaeus*, *Rhamnus Frangula*, *Sorbus Aucuparia*, and *Viburnum Opulus*; in the upper, and therefore more recent, part, which has had a warmer climate, we find *Alnus glutinosa*, *Cornus sanguinea*, *Crataegus monogyna*,

Corylus Avellana, *Tilia europaea*, *Ulmus montana*, etc. Here we come to the transition to the next flora.

(4) *Quercus Flora*, which immigrated during the warmest period after the Glacial Epoch, when the mean summer temperature was about 2.5°C . higher than at the present day. In addition to *Quercus pedunculata* and *Q. sessiliflora*, there immigrated during this period *Acer platanoides*, *Fraxinus excelsior*, *Hedera Helix*, *Viscum album*, and a great number of warmth-loving plants, which have since kept to the warm slates and limestones.

As the last immigrants during the steady decrease of the summer temperature, Gunnar Andersson gives

(5) The *Fagus Flora* and (6) the *Picea excelsa Flora*.

What is new in this theory is that there is assumed to have been only one period with higher temperature since the Glacial Epoch. This, too, is supported by the results at which W. C. Brögger ('00) has arrived in his investigations of the Quaternary fossil mollusc fauna in the south of Norway.

Since then, the question of the immigration of the flora into Sweden has been treated in a series of papers by R. Sernander ('10), who rather inclines to A. Blytt's theory, and in Norway by J. Holmboe ('03), who subscribes to that of Gunnar Andersson.

The geological basis, however, upon which all investigations of the immigration of the flora into the Scandinavian peninsula must be built, has of late years undergone considerable alteration. A number of recent discoveries of fossil plants also give new points of support. There is still, however, uncertainty concerning many points, so that the opinions of geologists and phytogeographers by no means coincide.

In the first place, by counting the layers in stratified clay deposits in Sweden, Gerhard de Geer ('08) has succeeded in proving that not more than about 12,000 years have elapsed since the ice-cap of the last Glacial Period extended as far as Skaane in the south of Sweden. The ice had taken about 4,000 years to withdraw thus far from its southernmost boundary in Germany, and it afterwards took as much as about 3,000 years to withdraw to a range of terminal moraines

in central Sweden, and in the south of Norway to the morainic ridges that extend from Fredrikshald to Moss, Horten, Arendal, etc., and are designated by the Norwegian word "Ra."

According to G. de Geer, these great terminal moraines must have been formed about 9,000 years ago when the inland ice stood still along that line for a period of about 350 years. It is a matter of indifference to us that other geologists believe that this "Ra" period occurred somewhat earlier.

What is of great importance in the immigration of the flora, however, is that the extreme southeast of Norway and the center of Sweden, at the time of the "Ra" formation, lay much lower than at the present time, and sank still lower some time after the ice withdrew. It is supposed that the sea near Kristiania, during the "Ra" period, was about 660 feet higher than it now is, and a little later rose to 720 feet above its present height, which is the highest limit of the late glacial sea. But this limit differs in different parts of the country; it falls toward the coast, especially toward the west coast of Norway. At Larvik, for instance, it is about 426 feet; at Arendal, 246 feet; at Kristianssand, about 130 feet; at Mandal, 82 feet; and at Farsund, only 28 feet. Farther north it increases again, so that at Kristianssund it is about 246 feet, and at Trondhjem, 650 feet, or almost as great as at Kristiania.

THE DRYAS PERIOD

I have previously ('05) endeavored to show by *Dryas* and *Salix polaris*, which A. G. Nathorst has found in a fossil state in the south of Sweden, that the arctic flora cannot have made its way thence into Norway; for during the "Ra" formation the masses of ice went right out into the sea, and when the ice had withdrawn far enough to leave open land within the "Ra" line, the climate had already altered to such an extent that the arctic flora was extinct in the south of Sweden.

The earliest plants of which J. Holmboe ('03) has found remains in the southeast of Norway, prove also to be sub-

alpine; but farther west fossil arctic plants have been found in a number of places.

D. Danielsen ('09, '12) has found, between Kristianssand and Mandal, fossil leaves of *Salix polaris* from 46 to 59 feet, *Dryas octopetala* from 46 to 52 feet, and *Betula nana* from 46 to 52 feet above the sea. The uppermost marine boundary here is from 137 to 141 feet above sea-level, but the leaves are supposed to have been carried out by currents and deposited at a depth of perhaps 65 feet. Something similar may have taken place with most of those subsequently mentioned, as they are sometimes found covered with more or less loose material.

C. F. Kolderup ('08) has found, near Bergen, *Dryas octopetala*, *Salix polaris*, and *S. reticulata*, from 115 to 130 feet above the sea, while the marine boundary lies at a height of about 190 feet above sea-level.

J. Rekstad ('05, '06, '07, '08) has found *Salix polaris* 130 feet above the sea in Söndfjord, 187 feet above the sea in Nordfjord (marine boundary 250 feet above sea-level), and in Nordmøre sometimes 82 feet, sometimes from 344 to 377 feet, above sea-level; and *Salix herbacea* in Nordfjord 220 feet above the sea (marine boundary 360 feet above the sea), in Söndmøre 85 feet.

K. O. Björlykke ('00) has found *Salix reticulata* near Kristiania 540 feet above the sea, and near Trondhjem 340 feet above sea-level.

P. A. Oeyen ('04, '07) has found *Dryas octopetala* and *Salix reticulata* near Trondhjem at a height of 557 feet above sea-level, and *Salix polaris* in Asker, near Kristiania, 600 feet above the sea (the marine boundary at the latter locality is 692 feet above sea-level).

Remains have also been found of species that may have a subalpine occurrence, such as *Betula nana*, *Juniperus nana*, and *Salix phylicifolia*; but as they are less conclusive, they are not included here.

The point of especial interest is that these fossil plants on the west coast are found with remains of the high arctic mollusc *Yoldia arctica*, which is not now found on the shores

of Norway, but on the coast of Spitzbergen, and indicates a mean temperature of from -3 to -7°C . and thus quite an arctic climate. At Kristianssand these arctic plant-remains are found together with remains both of *Yoldia arctica* and *Mytilus edulis*, while *Salix polaris*, near Kristiania, is found with *Mytilus* and far below the highest marine boundary.

Two questions now present themselves, (1) did *Salix polaris* and other arctic vegetation continue to live during the Last Glacial Period upon a stretch of coast in the west and north of Norway that was not covered with ice, or (2) did *Salix polaris* and the other arctic plants immigrate from Jutland—where they lived during the Last Glacial Period—to the first land from which the ice disappeared at Kristianssand, and thence spread along the edge of the ice on both sides as the latter disappeared?

I have previously endeavored to uphold the first of these views as the more probable, having found ('05, p. 337) that the discoveries hitherto made of the remains of arctic plants favored the belief that 'during the Last Glacial Period there lived in Norway a high-arctic vegetation upon a strip of coast that was free from ice and must have extended about as far down as the Sogne Fjord. Subsequently, as time went on, several species of high-arctic plants that had immigrated from Russia and Siberia made their way for a greater or smaller distance southward in the north of Scandinavia.'

Various later discoveries of arctic plants all the way down to the south point of Norway go to prove that the iceless margin of coast may have extended thus far, at any rate partially. The isolated occurrence of *Saxifraga aizoon*, growing upon the mountains in inner Ryfylke, east of Stavanger, is also difficult to understand unless it is assumed that it migrated thither from an iceless margin of coast, as this species, beyond being found in the Alps, is only known in Nordland in Norway, and in Iceland and Greenland.

But it seems probable that here a number of vegetable species from the interglacial period may have survived the Last Glacial Period. This must have been the case with

Artemisia norvegica, whose province of distribution in Norway is on the Dovre and adjoining mountains in the north-west (Troidheimen), some of which could scarcely have been covered with ice during the Last Glacial Period. It is even possible to name, with considerable accuracy, some of these plants, as they form the "Greenland element" in the arctic flora of Norway. I designate as such those plants which Norway has in common with Iceland, Greenland, or the north of North America, but that are not found in western Siberia. These are as follows:

Arnica alpina is found in the north of Norway from Salten to Alten, and also in the north of Sweden, on the Kola Peninsula and Novaja Semlja, but not again until the east of Siberia is reached. It is also found in Greenland and on the Alps.

Campanula uniflora is found in Norway from Lom to Reisen, in Swedish Lapland and Novaja Semlja, but elsewhere only in Greenland and arctic North America.

Carex nardina is found in Norway from Salten to Kvaengen, and in Swedish Lapland, but elsewhere only in Iceland, Greenland, and arctic North America.

Carex scirpoidea is known in Norway in Salten, and elsewhere only in eastern Siberia and western Greenland.

Draba crassifolia is found in Norway, 'round Tromsö, but otherwise only in Greenland.

Pedicularis flammea is found in Norway from Salten to Lyngen, and in Swedish Lapland, but elsewhere only in Iceland and Greenland.

Platanthera obtusata is found in Norway in Reisen and Alten, but otherwise is known only from eastern Siberia and arctic North America.

A fact that possesses peculiar interest in the study of the occurrence of these and other similar species of plants in the Norwegian mountains, is the discovery in central Norway of interglacial remains of *Elephas primigenius* and *Ovibos moschata*. These great mammals became extinct at the beginning of the Last Glacial Period, but some of the plants that lived at the same time found a dwelling place upon the iceless

coast margin and there managed to survive that period, and then to some extent followed the retreating ice up to the mountains where they are now found.

Andr. M. Hansen ('04, '04^a) even assumes that at least 300, perhaps as many as 500, kinds of vascular plants may have lived upon this supposed iceless strip of coast, which he assumes to have been fairly broad. These figures are perhaps rather high, but it is not possible to make more exact statements until paleobotanical investigations have been carried out in the peat-bogs in these regions.

Against the second possibility, namely, that the arctic plants may not have immigrated from Denmark to Kristianssand until after the ice had withdrawn, several facts may be cited.

These arctic plants, farther up the west coast of Norway (e.g., in Nordfjord), are found together with *Yoldia arctica*, and thus in a decidedly arctic climate, while those near Kristianssand, though, indeed, found with *Yoldia*, also occur with *Mytilus*, which indicates that the climate was somewhat milder and that the plants originated at a more recent period than those in Nordfjord. Thus the arctic plants, e.g., those in Nordfjord, cannot have immigrated thither from Kristianssand, but may be assumed to have been there during the Last Glacial Period.

On the other hand, *Salix polaris* near Kristiania, which appears to have originated at a somewhat later period, may have been able to immigrate thither along the margin of the ice from Kristianssand; but this cannot at present be stated with certainty, as no fossils have been found between the two points.

THE BETULA ODORATA PERIOD

As the ice-cap withdrew and the climate became milder, the land began to rise. In the center and south of Sweden, this took place so rapidly that a land connection was formed between Sweden and Denmark, and also between south and north Sweden, very much as it is at present. The Baltic thereby became a lake, its waters becoming gradually fresher and containing fresh-water animals, especially *Ancylus fluvia-*

tilis, which has given to this geological period the name of the Ancyclus Period.

By this upheaval of the land, a broad migration road for



Fig. 4. Map of Scandinavia during the Ancyclus Period: the white area represents the remainder of the great ice sheet; region indicated by parallel horizontal lines represents lake (water); region indicated by oblique cross-lines represents land.—Chiefly after De Geer.

plants was opened from the southeast and east to Norway. Seeds were probably carried over now and again before this upheaval of the land—as soon as land was vacated by the

ice in the southeast of Norway; but the direct land connection facilitated the spread of all species of plants.

Betula odorata was an early immigrant, and with it were a number of other plants of which fossil remains have been found, especially in peat-bogs in the southeast of Norway,¹ namely, *Betula nana*, *Carex ampullacea*, *C. filiformis*, *Cicuta virosa*, *Comarum palustre*, *Empetrum nigrum*, *Equisetum fluviatile*, *Hippuris vulgaris*, *Juniperus communis*, *Menyanthes trifoliata*, *Myriophyllum spicatum*, *Nymphaea alba*, *Potamogeton natans*, *Scirpus lacustris*, *Vaccinium Vitis-Idaea*, *Zannichellia polycarpa*.

But in addition to these, it may probably be assumed that the following species, which are found as subfossil remains from the subarctic or partially arctic period in Swedish peat-bogs,² may have migrated into Norway by this southeastern road as soon as some of the nearest land areas were free from ice. These are *Andromeda polifolia*, *Arctostaphylos alpina*, *A. Uva Ursi*, *Batrachium confervoides*, *Diapensia lapponica*, *Montia fontana*, *Myrtillus uliginosus*, *Oxyria digyna*, *Phragmites communis*, *Polygonum viviparum*, *Populus tremula*, *Potamogeton filiformis*, *P. praelongus*, *Salix aurita*, *S. caprea*, *S. cinerea*, *S. phyllicifolia*, *S. repens*, *Scheuchzeria palustris*, and *Stachys sylvatica*. During this period *Hippophaë rhamnoides* also immigrated to Sweden, but as it spread along the east coast of that country and thence through Jemtland to the north of Norway, this could not have taken place until much later, after the last of the central inland ice had melted.

THE PINUS SYLVESTRIS PERIOD

After *Betula odorata*, but during the so-called Ancyclus Period in Sweden, *Pinus sylvestris* migrated to the southeast of Norway, while the climate was still comparatively cold; but, as we may gather from some of the plants that occur, especially in the latter part of the pine zone, the temperature became rather rapidly warmer.

J. Holmboe has found in the peat-bogs of Norway the following fossil plants in the pine zone: *Alisma Plantago*, *Alnus*

¹ By J. Holmboe ('03).

² By Gunnar Andersson ('96).

glutinosa, *A. incana*, *Andromeda polifolia*, *Betula verrucosa*, *Carex Pseudocyperus*, *Cladium Mariscus*, *Corylus Avellana*, *Eriophorum vaginatum*, *Isoetes lacustris*, *Linnaea borealis*, *Lycopus europaeus*, *Naias marina*, *Nuphar luteum*, *Oxycoccus microcarpus*, *Rhamnus Frangula*, *Rubus Idaeus*, *Salix aurita*, *Scheuchzeria palustris*, *Solanum Dulcamara*, *Spiraea Ulmaria*, and *Ulmus montana*.

In addition to these, Gunnar Andersson has found in Swedish peat-bogs from the pine period the following species: *Calla palustris*, *Caltha palustris*, *Carex riparia* (?), *C. vesicaria*, *Ceratophyllum demersum*, *Cornus sanguinea*, *Crataegus monogyna*, *Eriophorum angustifolium*, *Galium palustre*, *Iris Pseudacorus*, *Myriophyllum alterniflorum*, *Naias flexilis*, *Myrtillus nigra*, *Naumburgia thyrsiflora* (?), *Oxalis Acetosella*, *Pedicularis palustris*, *Potamogeton pectinatus*, *Prunus Padus*, *Ranunculus repens*, *Rubus saxatilis*, *Rumex Hydro-lapathum*, *R. maritimus*, *Sorbus Aucuparia*, *Sparganium ramosum*, *Thalictrum flavum*, *Tilia cordata*, *Viburnum Opulus*, and *Viola palustris*.

But several of these latter species did not get as far as Norway until the succeeding warmer period, and we shall therefore find them again in the list of fossils that have been found in peat-bogs from the Oak Period. A few of them may also have immigrated by other routes, as a land connection with Sweden was established not only in the south but also in the east, the ice having withdrawn to the interior of the country, and at the close of the Ancyclus Period probably melted away entirely. Various discoveries go to prove, for instance, that *Alnus glutinosa* migrated into Norway from the south, while *Alnus incana* came from the east.

There are in Norway two quite distinct forms of *Pinus sylvestris* L., which by some botanists are given as species, namely, var. *septentrionalis* Schotte, and var. *lapponica* (Fr.) Hn. The second of these, which is found in abundance in Finland and the far north of Sweden, also grows in Norway, especially in the north, and on the mountains farther south, where here and there it pushes down into the valleys. It may be assumed that this *P. sylvestris* var. *lapponica* did not im-

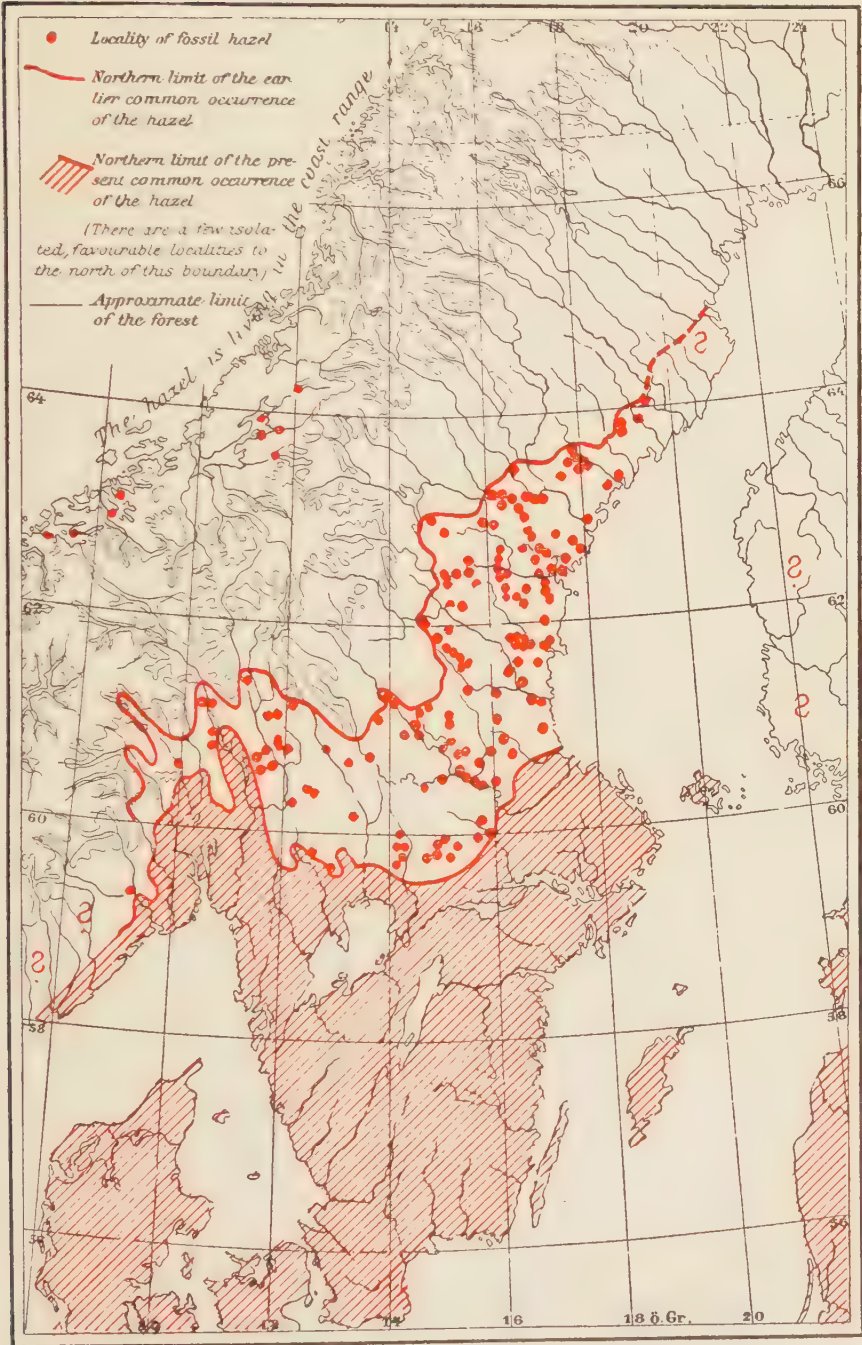
migrate from the northeast until much later—after the ice-cap had melted in the north of Norway and Sweden, and then made its way southward. The common *Pinus sylvestris*, on the contrary, as we have said, undoubtedly migrated into Norway from the southeast through Sweden, which is probably the way by which most of those species immigrated which are now found growing with it in the southeast of Norway.

THE QUERCUS PEDUNCULATA PERIOD

The climate gradually becomes warmer, the inland ice has quite disappeared, and simultaneously with its disappearance the land in a belt across central Sweden begins once more to sink (the Littorina Subsidence). When this subsidence culminated, the south of Sweden was a great island which, on the south, was separated—as it now is—from Denmark by Oeresund and by a broad arm of the sea, which ran from Skagerak through the district in which the lakes Venern and Vettern now lie right to the Baltic. This sea thus acquired an opening into the North Sea, and its waters gradually became salt.

This subsidence of the land, which took place when the land around Kristiania was about 230 feet lower than it now is, did not greatly affect Norway, for it amounted in the latter to only a few yards. But it may probably be assumed that so great an arm of the sea, with a current of Gulf Stream water that even brought Gulf Stream nuts (*Entada gigalobium*) with it to the shores of Bohuslaen—whence they are not carried at the present day—must have made the climate warmer and more insular than it now is. Before the subsidence, then, the climate must have been warm and dry, after the subsidence, warm and damp.

How much warmer the climate must have been is apparent from Gunnar Andersson's investigations—following the discovery of fossils—on the distribution of *Corylus Avellana* at that time, compared with its present distribution. It appears that the mean temperature of the summer months must have been about 2.5 C. higher than it now is. In the sea off the coast of Norway there lived at that time species of the more



southern mollusc genus *Tapes*, which shows that the average annual temperature must have been between 8 and 9°C. (Brögger, '00).

Various opinions have been expressed as to whether the warmest period was before, at, or a little after, the maximum of the Littorina Subsidence in Sweden. This is of little importance here, but what is more important is that the earliest remains of stone implements in Norway date from this warmest period (the Tapes Period), which, therefore, in the opinion of archaeologists, must be assumed to have been about 7,000 years ago. This accords well with G. de Geer's calculations from the number of clay strata.

J. Holmboe has found the following species of plants, together with *Quercus pedunculata*, in Norwegian peat-bogs: *Acer platanoides*, *Aspidium Thelypteris*, *Bidens cernua*, *B. tripartita*, *Calla palustris*, *Carex stellulata*, *C. vesicaria*, *Ceratophyllum demersum*, *Crambe maritima*, *Fraxinus excelsior*, *Galeopsis Tetrahit*, *Iris Pseudacorus*, *Myrica Gale*, *Najas flexilis*, *Naumburgia thyrsiflora*, *Oxalis Acetosella*, *Peucedanum palustre*, *Potamogeton praelongus*, *Ranunculus repens*, *Rubus fruticosus*, *Ruppia rostellata*, *R. spiralis*, *Scirpus maritimus*, *Sorbus Aucuparia*, *Sparganium ramosum*, *Stachys sylvatica*, *Thalictrum flavum*, *Tilia cordata*, *Viola* sp., *Zostera marina*.

It will at once be seen that a good many of these species were enumerated as having been found in the south of Sweden during an earlier period, i.e., with *Pinus sylvestris*. This agrees very well with the assumed immigration route through Sweden, as it must have taken a considerable length of time for these plants to spread through Sweden into southern Norway. It must not, however, be forgotten that the occurrences of plants in the peat-bogs indicate only the minimum length of time of their existence in the place in question, as they may very well have lived there for a long time before being deposited in a peat-bog, to be found there through the investigations of a botanist.

In addition to the above, Gunnar Andersson has found the following fossil species in the Oak Period in Sweden, these

species being either unknown in Norway or found only in later deposits, some of them probably not having immigrated until later, together with *Picea excelsa*. They are *Angelica sylvestris*, *Cakile maritima*, *Cornus suecica* (?), *Helianthus peplodes*, *Hedera Helix*, *Ledum palustre* (?), *Potamogeton crispus*, *Ranunculus Flammula*, *R. sceleratus*, *Sagittaria sagittifolia*, and *Viscum album*.

A. Blytt ('82) assumed that a great many warmth-loving species, constituting what he called the "boreal flora," must have immigrated at this time, especially several xerophilous plants, such as a number of *Labiatae*, *Boragineae*, etc. (some of which are now commonly found on the steppes of southern Russia), which still keep especially to warm slates and limestones in the Norwegian lowland in the east, the west, and the province of Trondhjem.

Andr. M. Hansen ('04) draws especial attention to the following among these species, constituting what he calls the "Origanum community," and which grow on open slopes with a very sunny exposure: *Agrimonia Eupatoria*, *Androsace septentrionalis*, *Arenaria serpyllifolia*, *Calamintha Acinos*, *Campanula Cervicaria*, *Carex muricata*, *Centaurea Scabiosa*, *Dianthus deltoides*, *Echinospermum lappula*, *Origanum vulgare*, *Plantago media*, *Polygala amara*, *Ranunculus Polyanthemus*, *Torilis Anthriscus*, *Trifolium medium*, *Turritis glabra*, *Verbascum nigrum*, and *V. Thapsus*. As they grow upon dry slopes, it is not very probable that remains of them will be preserved in peat-bogs or elsewhere. Paleontologically, therefore, their immigration cannot be determined, but something may be concluded as to their occurrence in the present day; for it appears that this warmth-loving plant community has its most connected province of distribution from the lowlands of the southeast of Norway, on the warm slates through Valdres and Gudbrandsdal, and are then met with once more on the low land of the western fjord valleys, and in the province of Trondhjem. To this last locality there is evidently also an immigration road through Jemteland from the east coast of Sweden. On the other hand, this plant community is wanting throughout so great a part of the

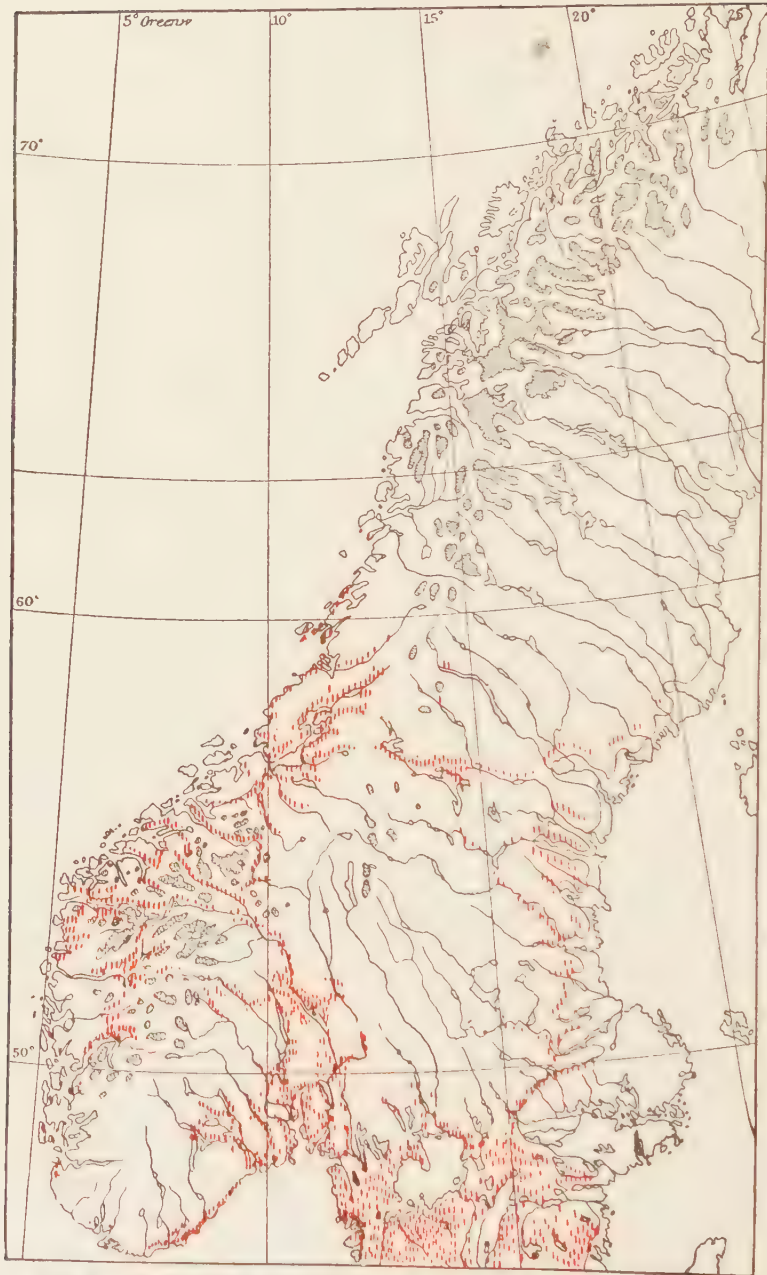


Fig. 6. Sketch-map showing the distribution and journeys of the *Origanum* community (vertical red lines) in Scandinavia. The extent of the montane region during the warmest post-glacial period is indicated by black-dotted areas.—After Andr. M. Hansen.

southwestern lowlands, that it can hardly be imagined that it migrated along the coast to the west and Trondhjem.

It must therefore be taken for granted that these plants migrated by way of the mountain passes, some of which now lie at such an altitude that even *Pinus sylvestris* cannot live in the highest localities. But I have already mentioned that the summer temperature during this period was about 2.5°C. higher than it now is. We see, moreover, that remains of pine forests are found on the mountains in Norway, e.g., on the Dovre Mountains in central Norway, and on the Hardanger plateau in the south of Norway, respectively 990 and 1,470 feet above the present highest limit of *Pinus sylvestris*. Under the then existing climatic conditions, the now treeless passes were clothed with forest, and warmth-loving plants were able to spread through them.

A. Blytt, and after him R. Sernander, distinguishes between a boreal and a sub-boreal flora, the members of which are supposed to have been lovers of warmth and dryness, but separated in their immigration by an Atlantic flora that loved humidity and warmth. With this I cannot agree. Several of the species that Blytt ('82) classes under "sub-boreal" are found in a fossilized state together with those he calls "boreal"; and around Kristiania many species of these so-called different floras grow together under exactly the same conditions in the same localities.

It seems likely, however, that the climate was more humid during the Littorina Subsidence, when the water of the Gulf Stream could make its way directly into the Baltic across central Sweden. A. Blytt ('82, p. 23) says: "Man darf deshalb mit einem hohen Grad von Wahrscheinlichkeit behaupten, dass die atlantische Flora in dieser Regenzeit eingewandert ist, und ihren Weg rund um den Christianiafjord gefunden hat (in derselben Weise, wie unter der folgenden Regenzeit die subatlantische)." I cannot agree in all respects with this. Those forms which Blytt calls "atlantische Arten" include a great number of species, of which some occur in what I have here called the "region of *Ilex Aquifolium*," others constitute what I have called the "west European

coast flora," while among other species belonging to Blytt's group *Rhynchospora alba*, *Alnus glutinosa*, *Myrica Gale*, *Arnica montana*, *Erica Tetralix*, *Ranunculus Flammula*, *Lychnis Flos-cuculi*, etc., may be mentioned, which grow on the low-lying land in many parts of southern Norway. As a rule, they prefer, it is true, damp places, but some species go right up to the Birch Zone on the mountains, so they may be presumed to have immigrated from the southeast through Sweden; but there is nothing to prove that this took place just at the maximum of the Littorina Subsidence. As instances, indeed, of the contrary, *Alnus glutinosa* from the Birch Period and *Myrica Gale* from the Oak Period are found in Norwegian peat-bogs and were, therefore, much earlier.

I believe that the west European coast flora on the west coast of Norway immigrated directly, by fits and starts, from England; but we will return to this later on.

THE PICEA EXCELSA PERIOD

According to archaeological calculations, the Scandinavian Stone Age lasted about 3,000 years, so that the Bronze Age in Scandinavia began about 4,000 years ago. During this period the climate was undoubtedly warmer than it now is, and it was not until the Bronze Age that any noticeable fall seems to have taken place.

At the beginning of the Stone Age the land around Kristiania lay 230 feet lower than at present, but during the Stone Age it was elevated about 184 feet, and during the Bronze Age it rose to about its present height above sea-level.

In the Bronze Age, or perhaps in the latter part of the Stone Age, *Picea excelsa* migrated into Norway from the east, from Finland through Sweden. In Finland it is still found as a fossil in the Oak Period, and in Sweden, especially in the north and east, it is so found, while spruce is not found fossilized in the south of Sweden or Denmark after the Glacial Epoch.

In the north of Norway (Finmark) there are occurrences of spruce that are entirely independent of the spruce's great province of distribution in the south of Norway. It appears

that these northern occurrences are of a distinct form (*Picea excelsa* [Lam.] Link f. *obovata* Ledeb.), which is classed by some botanists as a separate species, and has its distribution through the north of Finland and Russia. There can, of course, be no doubt that the spruces in these northernmost occurrences immigrated independently from Finland, and probably at a later period, as there is a tradition that they were imported thither by human beings (Lapps).

According to J. Holmboe, *Calluna vulgaris* came into Norway during the same recent period in which *Picea excelsa* made its appearance, but there is no doubt that the former immigrated from the west and then spread eastward, i.e., in the direction opposite to that in which *Picea excelsa* spread. Both these species have now a very wide distribution in Norway.

Strange to say, there has not been found in the deposits from the Pine Period in Norwegian peat-bogs a single plant that is not to be found in the earlier periods. In Sweden the only new species found is *Rubus Chamaemorus*, which, however, undoubtedly grew there long before, as it must on the whole be considered to be a subalpine species. This is sufficient to show that special conditions are necessary in order that parts of plants may be preserved in bogs, and that it will, therefore, always be only a small proportion of the plants growing around the bogs which will be so preserved.

It is strange, for instance, that *Taxus baccata* is not found in Norwegian peat-bogs. It is found as a fossil from the Oak Period in Sweden, and must have been far more common in Norway in the early Iron Age than it is at the present time, as H. Convents found, on examining twenty-three vessels in the Archaeological Museum in Kristiania, that eighteen of them were of *Taxus* and only one of *Picea excelsa*.

According to R. Sernander ('10) the period of greatest warmth must have occurred in the Bronze Age, and he believes that it was then that *Corylus Avellana* was most widely distributed northward. The Bronze Age, however, judging from the molluscs that were then found off the south coast of Norway, seems to have had a cooler climate than that of the

Tapes Period, i.e., the Scandinavian Paleolithic Age. On the other hand, R. Sernander believes that at the beginning of the Iron Age—about 2,400 years before our own day—so great a decline in temperature ensued that the montane plants made their way into the lowlands in many places. He interprets the present occurrences of alpine plants in the lowlands as relics from that period. This can, however, be the case only to a certain extent, for there is no doubt that at the present day alpine plants spread down to the lowlands and continue to grow there, provided the conditions are favorable. R. Sernander gives to his assumed cold, damp period at the beginning of the Iron Age the name employed by A. Blytt, the “sub-Atlantic period”; but the two have, in reality, very little to do with one another. A. Blytt states that his sub-Atlantic period occurred when the south coast of Norway lay from 30 to 50 feet lower than its present level, which would answer to the beginning of the Bronze Age. He mentions, among other species that immigrated during the sub-Atlantic period, *Carex Pseudocyperus* and *Cladium Mariscus*, which had already immigrated in the Pine Period, and *Ceratophyllum demersum*, which had immigrated in the Oak Period, besides two or three species that were certainly imported later in foreign grain and grass seed.

I do not yet consider R. Sernander's cold, damp “sub-Atlantic period” at the beginning of the Iron Age to have been clearly proved, although there are a few facts that speak in its favor. But even if such a cold, damp period did supervene, its principal effect would have been to decimate the oak flora—in localities that were not especially warm—more rapidly than if the climate had gradually become colder from the Stone Age to the present time, as most people believe. Similarly, it may have promoted the occasional descent of montane plants to the lowlands, but it appears that this can also take place under the present climatic conditions, without the necessity of having recourse to relic occurrences from the “sub-Atlantic” or even from the “Dryas Period.”

An instance of such an occurrence is that of *Dryas octopetala* at Langesund in southeastern Norway. This species

is found there right down to the level of the sea, and is very common on the limestone of the locality. Together with J. Holmboe ('03), I have endeavored to prove that over the whole of the area in which *Dryas* appears, the latter can scarcely have existed for more than 100 years. I cannot ascribe any convincing power to the objections that have been raised against this line of argument.

THE FAGUS SYLVATICA PERIOD

In Norway, as already mentioned, *Fagus sylvatica* grows upon the southeast coast, with Larvik as a center. There is, in addition, an isolated beech-wood in Seim, to the north of Bergen, 280 miles from the nearest occurrence of beech.

It was formerly believed by A. Blytt that this beech-wood in Seim was a relic of a connected distribution of beech along the coast; but no discovery of fossils favors this idea. On the contrary, these two occurrences of beech appear to be perfectly independent of one another.

J. Holmboe ('05, '09) has endeavored to find out when the beech appeared at Larvik and in Seim. He has come to the conclusion, judging from what has been found in the peat-bogs, that at Larvik the beech immigrated considerably later than *Picea excelsa*. It can thus actually be assumed to have immigrated in the Iron Age, or perhaps as late as the time of the Vikings. This late immigration is in harmony with the fact that in the southeast of Norway the beech is making very rapid advance at the present time. Holmboe says that the beech-wood in Seim, from a geological point of view, is very recent, but that in any case its age should scarcely be put lower than about 1,000 years.

It seems to me most probable that the beech was introduced into Norway by man in the time of the Vikings, when there was ample communication with those countries in which this so generally useful tree formed extensive forests. In Seim, near Bergen, where the beech grows, the Norwegian King Haakon the Good, who was educated in England at the court of King Athelstan, and reigned from 935 to 961, had one of his estates; and it is not unnatural to suppose that he may

have tried to introduce a tree that he knew so well from his childhood and youth in England.

It is certain that in the course of time man has assisted in introducing many species of plants, some consciously, as, for instance, plants for cultivation, others by chance and unconsciously.

In the famous Viking ship from Oseberg, which is believed with certainty to have originated in the first half of the ninth century, fruit, seeds, and other remains of plants have been found, and have been determined by J. Holmboe ('06). The following cultivated plants were among them: *Avena sativa*, *Corylus Avellana*, *Isatis tinctoria*, *Juglans regia*, *Lepidium sativum*, *Linum usitatissimum*, *Pirus Malus*, and *Triticum vulgare*. As *Isatis tinctoria* is found growing apparently wild, in certain places in Norway, there can scarcely be any doubt that it has found its way thither from localities where it had previously been cultivated as a dye-plant. This is probably also the case with *Serratula tinctoria* in Jaederen, near Stavanger. The weeds found in the Oseberg ship were as follows: *Capsella Bursa-pastoris*, *Chenopodium album*, *Galeopsis Tetrahit*, *Lamium (purpureum?)*, *Polygonum Convolvulus*, *Stellaria media*, and *Urtica urens*. Several of these, it is true, had immigrated earlier, as has been said of *Galeopsis Tetrahit*; but it shows that as early as the time of the Vikings, there were opportunities of importing foreign weeds.

In monastery gardens various medicinal, household, and ornamental plants were cultivated, and one is inclined to believe that several of these which now have quite a wide distribution in Norway, e.g., *Aquilegia vulgaris*, *Berberis vulgaris*, *Sambucus nigra*, etc., originally spread with the monasteries as centers.

It is still easier to demonstrate a number of species of weeds that have been imported recently, and of which some appear to have a really astonishing power of spreading. J. Holmboe ('00) has traced the spread of the following weeds from the year when they were first observed in Norway: *Alyssum calycinum* (1857), *Anthemis tinctoria* (1772?, 1807), *Barbarea vulgaris* (1790), *Berteroa incana* (1826), *Bunias*

orientalis (1812), *Campanula patula* (1870), *Cerastium arvense* (1817), *Chrysanthemum segetum* (1704), *Cotula coronopifolia* (1875), *Conringia orientalis* (1859), *Erigeron canadensis* (1874), *Galinsoga parviflora* (1880), *Lepidium perfoliatum* (1875), *L. virginicum* (1889), *Matricaria discoidea* (1850), *Rudbeckia hirta* (1880), *Senecio viscosus* (1804-1808), *Thlaspi alpestre* (1874), and *Xanthium spinosum* (1872). Some of these plants are now among the most troublesome weeds in large and small areas in Norway.

There can, I suppose, be no doubt that man, directly and indirectly, in the 7,000 years in which he has lived in Norway and maintained a lively intercourse—especially during the last 2,000 years—with the rest of Europe, must have assisted in introducing a great number of plants in addition to the above named. Among the former may be mentioned *Agrostemma Githago*, *Anchusa arvensis*, *Anthemis arvensis*, *Avena fatua*, *Brassica campestris*, *B. nigra*, *Bromus secalinus*, *Carduus crispus*, *Centaurea cyanus*, *Chenopodium capitatum*, *C. hybridum*, *C. glaucum*, *C. polyspermum*, *C. rubrum*, *Cirsium arvense*, *Convolvulus arvensis*, *Euphorbia Helioscopia*, *E. Peplus*, *Fagopyrum tataricum*, *Fumaria officinalis*, *Galeopsis angustifolia*, *G. Ladanum*, *G. speciosa*, *Galium Aparine*, *G. Mollugo*, *Lolium temulentum*, *Matricaria Chamomilla*, *Raphanus Raphanistrum*, *Sinapis alba*, *S. arvensis*, *Sonchus asper*, *S. oleraceus*, *Spergula arvensis*, *Spergula vernalis*, *Thlaspi arvensis*, etc. In addition to these there are a great many species that are generally classed in the floras under the heading “run wild” or “perhaps originally run wild,” and concerning which it may certainly be assumed that they have been introduced by man’s mediation in some way or other.

It is no longer possible to maintain the old dogma which held that the entire plant community migrated step by step, like a regiment of soldiers, and took possession of the country under climatic conditions that were favorable to the various species, while the previous vegetation was decimated and only survived in especially favorable localities; for *vegetable*

species generally immigrate singly and independently of one another.

It is not only man that assists in carrying plants across large sea surfaces; the wind, ocean currents, and especially birds from time to time transport seeds and other parts of plants, which, under favorable conditions, continue to grow.

I will not here go further into this complex question in its entirety, but will refer to R. Sernander's ('01) detailed work on the conditions for spreading in a great number of Scandinavian plants. I must, however, mention a few examples of probable, or certain, chance distribution. At Vaage Lake, far up the valley Gudbrandsdal, 990 feet above sea-level and separated from the innermost fjords of the west coast by 56 miles of very high mountains, grows the typical sea-shore plant, *Elymus arenarius*. That this occurrence represents a relic is absolutely out of the question, for the sea cannot have reached the height of Vaage Lake since the Silurian Period. But I have seen gulls flying over the lake, and they may possibly have carried seeds with them, which have found a favorable soil in the long sandy shores.

In 1837, *Coleanthus subtilis* was found upon a flooded river bank a little north of Kristiania, and in 1842 a great number of specimens were collected in the same locality, probably all that existed there, for in spite of the most careful search for a number of years, the plant has never subsequently been found in that or in any other place in Norway. As its nearest habitat is in Bohemia, it can only be supposed that some wading bird, in rapid flight from Bohemia to Norway, brought the seed with it; and, furthermore, that as the seed fell upon favorable soil, the plant grew up and had already begun to spread when the collection was made in 1842.

I have already ('05) endeavored to show that *Campanula barbata*, which occurs in a limited area on the mountains of central Norway, and is not again found until we come to the mountains of Central Europe, cannot be a glacial relic, but must have been accidentally introduced into Norway (by birds?) in recent times.

Judging from the distribution in the present day of a number of plants on the south and west coasts of Norway, it seems natural to assume that they have been brought directly over the sea from the nearest country, Denmark or England. It was thus not necessary for them to move step by step by the long route through Sweden, or even round the Kristiania Fjord, to reach their present habitats. The latter is all the less probable from the fact that certain of them seem to have been imported quite recently, when the climatic conditions cannot have been very different from those which exist at the present time. The following are instances of these:

Aera setacea grows in Norway from Kristianssand to Stavanger. The species is common in Jutland in Denmark, but in Sweden is found only in the extreme south.

Airopsis praecox is found from Kragerö to Nordmøre. It occurs, it is true, in Sweden, from the south up to Vester-gothland and Bohuslän; but from that region to Kragerö is considerably farther than from Jutland, where the plant is found in abundance.

Corydalis claviculata is found from Kristianssand to Haugesund. It grows wild in Denmark and England, but not in Sweden; I assume, therefore, that it immigrated from one of the former countries.

Galium saxatile is found from Kristianssand to Nordmøre. It grows in Sweden from Skaane to Bohuslän, but it is far more probable that it came from Jutland, where it is common.

Genista tinctoria is found only at Brevik, and must have been recently imported, as there are only a few specimens of it. It is found wild only in southern Sweden, but is common in Jutland.

Geranium columbinum is found in the district extending from Kragerö through the west of Norway to the Trondhjem Fjord. In Sweden it has an eastern distribution from Skaane to Upland. It is common in Denmark.

Heracleum australe is found from Kragerö to Söndfjord. It occurs in Sweden from the south right up to Vermeland, but the distance from this district to Kragerö is considerably greater than that from Jutland, where it also occurs.

Hydrocotyle vulgaris grows here and there from Larvik to Bergen. In Sweden it does not extend farther than to Dalsland, but it is exceedingly common in Jutland.¹

Hypericum pulchrum grows in the region extending from Larvik through the west of Norway to the Trondhjem Fjord. In Sweden it is found from Halland to Bohuslän, but it is more natural to suppose that it immigrated from Denmark or England, where it is common.

Luzula sylvatica grows along the coast from Arendal to Lofoten. It is found wild only in the south of Sweden, but is common in Jutland.

Rubus Radula is found from Kragerö to Mandal. In Sweden it is found from Skaane to Bohuslän, but is very common in Jutland.

Sarothamnus scoparius grows between Grimstad and Mandal. In Sweden it is wild only in the east. It is very common in Denmark.

Scirpus multicaulis grows at Arendal and in Jaederen. It is found in Sweden from Skaane to Vestergothland. It is common in Denmark.

Scirpus setaceus is found to the west of the Kristiania Fjord and more recently has been found also along the coast almost as far as Bergen. It is found in Sweden from Skaane to Bohuslän, but it can scarcely be supposed to have migrated thence to its most easterly occurrence in Norway, as the center of its distribution in Sweden lies farther south, and in Norway farther west. It seems, therefore, more probable that it has been brought to Norway directly from Denmark.

¹ Since writing the above, I have discovered *Hydrocotyle vulgaris* in a locality on Kirkeøen (Hvaler) in southeastern Norway. The locality lies about midway between the easternmost of the previously known Norwegian stations and the Swedish localities and might be looked upon as proof that the species in question had immigrated step by step through Sweden and not directly from Denmark. This, however, is not the case. On an excursion in 1907, I visited the exact spot where I later found *Hydrocotyle vulgaris* and I can maintain with certainty that *Hydrocotyle* was not growing there at that time. The plant has, therefore, been introduced into the locality in question since that date. My opinion, therefore, that *Hydrocotyle* has immigrated by leaps and bounds directly from Denmark into Norway, is only strengthened by this discovery.

Stellaria Holostea grows along the coast from Grimstad to Bergen. It is found in Sweden from Skaane to Bohuslän, but must have migrated into southern Norway from Denmark, where it is common.

Teucrium scorodonia is found from Lyngör to Flekkefjord. In Sweden it has probably only become wild, but in Denmark it is common.

Vicia cassubica is found from Kragerö to Kristianssand. In Sweden it is found from Skaane to Dalsland, but it is common in Denmark.

Vicia lathyroides grows along the coast from the Hvaler Islands farthest east off Norway, to Kristianssand. In Sweden, however, its distribution is easterly from Skaane to Upland, so it must be assumed that it migrated into Norway directly from Jutland in Denmark, where it is not uncommon.

It will be noticed that most of these plants which I assume to have immigrated directly from Denmark (Jutland) to the south of Norway, are either bog or leguminous plants, or are such as have small seeds or stone-fruits. The carriage across water surfaces of such plants as these one would imagine could most easily take place through chance transport by birds. The distance across the Skagerak from Denmark to Norway is about 93 miles, and according to J. A. Palmén ('76) there are regular lines followed by birds of passage from Jutland to Jaederen, as also one almost to Kristianssand and another to Risör, the very places which appear to be the center of the distribution of the majority of the above-named species which I assume to have come directly from Denmark.

It is still less probable that a number of plants that belong to the coast flora of Western Europe, and in Norway are found only in the extreme west, where the winter temperature is unusually mild (from $+1$ to $+2^{\circ}\text{C.}$), should have immigrated from England via Denmark and Sweden, where they do not now grow, or at any rate grow only in the extreme south. If they did make such a journey, the climate must have been so much milder in the southeast of Norway that the warm period that is proved in the Stone Age would not have gone nearly far enough. A climatic change as violent

as this would have been, and that in a comparatively very recent geological period, is not probable, nor is it necessary to assume it in order to explain the occurrence of these plants in the west of Norway, if only one does not blindly adhere to the dogma that plants can migrate only step by step.

As instances of plants which I assume have migrated from England direct to the west of Norway, the following may be mentioned:

Asplenium Adiantum nigrum is rare from Jaederen to Kristianssund. It is found in England, but only in the very east of Denmark and the extreme south of Sweden; immigration from the two last-mentioned countries seems, therefore, to be out of the question.

Asplenium marinum grows in the west of Norway from Mosterö to Stadt. It is found in England, but neither in Sweden nor Denmark.

Erica cinerea grows on the outermost islands from Farsund to Söndmöre. It is found in England, but in neither Sweden nor Denmark.

Hymenophyllum peltatum grows in the outermost coast districts from Farsund to Nordfjord. It is found in England, but neither in Sweden nor Denmark.

Scilla verna grows in the extreme coast regions from Söndfjord to Söndmöre. It is found in England, but neither in Sweden nor Denmark.

Scolopendrium vulgare is found in two or three places between Hardanger and Söndfjord. It is common in England, but it is doubtful whether it has grown in Denmark, and in Sweden it is found only in the extreme east, in Gothland.

Vicia Orobus grows farthest west, from Lister and Jaederen to Söndmöre. It is common in England, but is not found in Sweden, and only here and there in Jutland. It might thus be supposed to have come from Denmark direct to Norway, but in that case it would probably grow a little farther south than it does. I consider it, therefore, most probable that it came over from England to the coast of Norway, and then spread

along the coast southward and northward to its present limits.

It also appears, according to I. Hagen ('12), that the case is similar with regard to a number of mosses, a direct migration from England to Norway being assumed. Hagen has so little faith, however, in the ability of these plants to migrate by leaps and bounds, that he supposes a post-glacial land connection with England, over which migration might gradually take place.

This land bridge between Norway and England was originally hypothetically constructed for the pre-glacial times by L. Stejneger ('07), who considers it necessary on zoögeographical grounds. At the conclusion of his paper he says:

"I think I may safely claim to have made it appear probable:

"1. That if the characteristic and important portion of the animals and plants of west Norway, called the 'Atlantic' biota, invaded that country from Scotland, it came by way of a land bridge connecting northern Scotland with western Norway north of 59° north latitude.

"2. That this land bridge existed after the first (Scandinavian) great glaciation.

"3. That part of this biota surely survived the second (Scandinavian) glaciation along the west coast of Norway, and that possibly the climate was not too severe for all to survive.

"4. That there is a possibility of a reestablishment of the land bridge during the 'Upper Forestian' stage with its congenial, more continental climate, during which the tenderer species may have immigrated, in case it should be proven that they could not have come with the hardier ones."

As will appear from the foregoing pages, I have also maintained ('05) that during the Last Glacial Period there was a stretch of coast in Norway that was free from ice, where some arctic plants, and, of course, also animals, were able to survive that period.

Since then Gunnar Andersson and Selim Birger ('12) have endeavored to give to the facts that favor this view the interpretation that the entire arctic flora element must have immigrated through Sweden, and followed the receding margin of ice. I consider their arguments on this point so unconvinc-

ing, especially in view of the most recent discoveries of fossil arctic plants, and my own observations of the rock formations in the west and north of Norway, that I have come to the conclusion that this iceless strip of coast was broader than I formerly supposed, and extended to the extreme southern point of Norway. In this respect my view is thus in perfect accordance with that of Stejneger.

As to whether there was an interglacial direct land connection between England and Norway, as Stejneger assumes, I cannot express an opinion, but I do not, in any case, consider it necessary for botanical reasons, although I am inclined to believe that the assumption of Stejneger will prove to be correct. On the other hand, I consider a post-glacial land connection between England and Norway, concerning which Stejneger himself is much in doubt, to be quite out of the question. There is nothing that can be brought forward to prove that previous to the post-glacial subsidence the land lay high enough for any real land bridge between Norway and England to exist. On the other hand, there are several facts that go to show that the southern part of the North Sea has lain higher than it now does, so that even considerable portions that are now under the sea were clothed with forest. This may possibly to some extent have diminished the distance between England and Norway; but the deep Norwegian Channel outside the coast of Norway has certainly been in existence ever since the Last Glacial Period.

But a land connection is not necessary to explain why the few species of plants that Norway and England have in common, and that must be assumed to have migrated over the North Sea, were able to come over in the course of the last 7,000 years. It must not be forgotten that according to J. A. Palmén ('76) there are two lines followed by birds of passage between England and the west of Norway; and that there may also have been other chance means of transport.

All things considered, I am inclined to believe that in trying to explain the distribution of vegetable species and the paths they have followed, we shall arrive at better results by studying the ways in which they spread at the present time than

by setting up hypotheses of tremendous convulsions of nature such as elevated and depressed land connections, climatic changes from cosmic causes, the oscillatory movement of the poles, etc., which can neither be proved nor disproved, as they lie beyond the spheres in which our present knowledge has a firm foundation on which to stand.

LITERATURE CITED

- Andersson, G. ('96). Svenska vaextvaerldens historia. Stockholm, 1896.
- , ('06). Die Entwicklungsgeschichte der Skandinavischen Flora. Congres Internat. Bot., Wien, 1905, Resultats scientifiques 45–97. f. 1–30. 1906.
- , ('09). Swedish climate in the late Quaternary period. Sveriges Geologiska Undersökning. Aarbok 1909:1–88. pl. 1–2. f. 1–11. 1909.
- , och Birger, S. ('12). Den norrlandska florans geografiska foerdelning och invandringshistorie med saerskild haensyn till dess sydiskandinaviska arter. Norrlandskt Handbibliothek v. Upsala & Stockholm, 1912.
- Areschoug, F. W. ('66). Bidrag till den skandinaviska vegetationens historia. Lunds Univ. Aarsskrift 1866:—. 1866.
- Björlykke, K. O. ('00). Glaciale plantefossiler. Naturen 1900:—. 1900.
- Blytt, A. ('76). Essay on the immigration of the Norwegian flora during alternating rainy and dry periods. Kristiania, 1876.
- , ('82). Die Theorie der Kechselnden kontinentalen und insularen Klimate. Bot. Jahrb. 2:1–50. 1882.
- , ('82). Nachtrag zu der Abhandlung: Die Theorie der wechselnden kontinentalen und insularen Klimate. *Ibid.* 2:177–184. pl. 1. 1882.
- , ('83). Om vexellagring og dens mulige betydning for tidsregningen i geologien og laeren om arternes forandringer. Videnskabsselskabets Forhandling 1883:1–31. f. 1–2. 1883.
- , ('06). Haandbog i Norges Flora. Udgivet ved Ove Dahl. Kristiania, 1906.
- Brögger, W. C. ('00). Om de sen glaciale og postglaciale nivaeforandringer i Kristianiafeltet (molluskfaunan). Norges geologiske undersøgelse 31:—. 1900–1901.
- , ('05). Strandliniens beliggenhed under stenalderen. I. Det sydoestlige Norge. Norges geologiske undersøgelse 41:—. Kristiania, 1905.
- Danielsen, D. ('09). Glacialgeologiske undersøkelser omkring Kristianssand. Nyt Mag. 47:23–95. pl. 1–4. 1909.
- , ('12). Kvartærgeologiske streiftog paa Soerlandet. Nyt Mag. 50:263–382. pl. 7–9. 1912.
- de Geer, G. ('08). On late Quaternary time and climate. Geologiska föreningen i Stockholm foerhandlingar. 30:—. 1908.
- , ('10). A thermographical record of the late Quaternary climate. Die Veränderung des Klimas. Stockholm, 1910.

- Hagen, I. ('12). Geografiske grupper blandt Norges loevmosser. *Naturen Aarg.* 36:—. 1912.
- Hansen, A. M. ('04). Hvorledes har Norge faaet sit Plantedaekke. *Naturen* 1904:—. 1904.
- , ('04a). Landnaam i Norge. En Utsigt over Bosaetningens Historie. Kristiania, 1904.
- , ('13). Fra istiderne. Soerlandet. Videnskabsselskabets Skrifter. I. Math.-nat. Kl. 1913²:—. 1913.
- Helland, A. ('12). Traegraenser og Sommervarmen. *Tidsskrift for Skogbruk.* Aarg. 20:—. 1912.
- Holmboe, J. ('00). Nogle ugraesplanters indvandring i Norge. *Nyt Mag.* 38: 129-262. f. 1-3. 1900.
- , ('03). Planterester i Norske torvmyrer. Et bidrag til den norske vegetations historie efter den sidste istid. Videnskabsselskabets Skrifter. I. Math.-nat. Kl. 1903²:—. 1903.
- , ('05). Studier over norske planters historie. II. *Nyt Mag.* 43:33-60. 1905.
- , ('06). *Ibid.* III. *Ibid.* 44:61-74. 1906.
- , ('09). Boegeskogen ved Lygrefjord i Nordhordland. *Bergens Mus. Aarbog* 1908¹⁸:—. 1909.
- , ('13). Kristtornen i Norge. En plantegeografisk undersoekelse. *Ibid.* 1913²:—. 1913.
- Kolderup, C. F. ('08). Bergensfeltet og tilstoedende trakter i senglacial og postglacial tid. *Bergens Mus. Aarbog* 1907¹⁴: 1-266. pl. 1. f. 1-38. 1908.
- Nathorst, A. G. ('71). Om naagra arktiska vaextlemningar i en soettvattenslera vid Alnarp i Skaane. *Lunds Univ. Ars-skrift* 1870:—. 1871.
- Oeyen, P. A. ('04). *Dryas octopetala* L. og *Salix reticulata* i vort land foer indsjoepperioden. Videnskabsselskabets Forhandlinger 1904¹: 1-6. 1904.
- , ('07). Skjaelbanke-studier i Kristiania omegn. *Nyt Mag.* 45:27-67. f. 1-3. 1907.
- Palmén, J. A. ('76). Ueber die Zugstrassen der Vögel. Leipzig, 1876.
- Rekstad, J. ('05). Jagttagelser fra terrasser og strandlinjer i det vestlige Norge. I. *Bergens Mus. Aarbog* 1905²: 1-46. pl. 1. f. 1-12. 1905.
- , ('06). *Ibid.* II. *Ibid.* 1906¹: 1-48. pl. 1. f. 1-19. 1906.
- , ('07). *Ibid.* III. *Ibid.* 1907⁰: 1-32. pl. 1. f. 1-15. 1907.
- , ('08). Bidrag til kvartaertidens historie for Nordmör. 1908.
- Sernander, R. ('01). Den skandinaviska vegetationens spridningsbiologi 1-459. f. 1-32. Upsala, 1901.
- , ('10). Die schwedischen Torfmoore als Zeugen postglazialer Klimaschwankungen. Die Verändr. des Klimas. Stockholm, 1910.
- Stejneger, L. ('07). The origin of the so-called Atlantic animals and plants of western Norway. *Smithsonian Misc. Coll.* 48: 458-514. pl. 67-70. f. 1-2. 1907.
- Wille, N. ('05). Om Indvandringen af det arktiske Floraelement til Norge. *Nyt Mag.* 43:315-338. 1905.
- , und Holmboe, J. ('03). *Dryas octopetala* bei Langesund. Eine glacielle Pseudorelikte. *Nyt Mag.* 41:27-43. 1903.

THE PHYLOGENETIC TAXONOMY OF FLOWERING PLANTS

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I. GENERAL DISCUSSION

Seventeen years ago in presenting a somewhat similar paper¹ to a smaller body of botanists, I began by saying that "it is as yet impossible to present a complete phylogeny of the angiosperms," and then a little later, "it will be many a year before the direct evidence we so much desire will leave no considerable gaps," and I am impelled to use the same words now as I begin this discussion to-day. For, while in this interval paleontology has uncovered many important facts whose significance is unmistakable, it is still true that there are "considerable gaps" in the record of the evolution of plants, both before and after the attainment of flower production. In other words, we are still in quest of direct testimony as to how flowers came into existence in particular, and as to the details of how and when they were modified afterwards. Yet we are not wholly without the direct testimony of the rocks in our inquiry as to the phyletic of the higher plants.

And I may be permitted here to enter a defense of such a discussion as I propose to make in this paper, in reply to those who think that since much of what I shall have to say is reached by a process of deduction, or, as it is more commonly called, speculation, it can have little scientific value. And I grant that in those fields where direct observation, experiment, and induction are possible there can be no defense of the exclusive deductive or speculative method. There are, however, many fields of botanical inquiry in which experiment is impossible, and observation is reduced to a minimum, and this

¹ Bessey, C. E. The phylogeny and taxonomy of angiosperms. (Address of the retiring president of the Botanical Society of America, at its third annual meeting, at Toronto, Canada, August 17, 1897.) *Bot. Gaz.* 24: 145-178. *f.* 1-3. 1897.

is necessarily the case when we are dealing with questions which relate to periods of time long past, as must be those involving phylogeny.

Moreover, it must not be forgotten that what I propose to do is after all much like what is done in even those sciences which we sometimes call the exact sciences. The ether of space, the undulatory theory of light, the tentative hypotheses as to the nature of electricity and gravitation, the form and extent of the universe, and the constitution of matter itself, are a few of the familiar speculations which physicists, astronomers and chemists have made parts of the conceptions of their respective sciences. To be sure, one can go but a short distance indeed in any science without finding it necessary to erect a speculative framework upon which to arrange his observed facts. As Jevons has so aptly expressed it in his 'Principles of Science' (2: p. 131):

"When facts are already in our possession, we frame an hypothesis to explain their mutual relations, and by the success or non-success of this explanation is the value of the hypothesis to be entirely judged. In the framing and deductive treatment of such hypotheses, we must avail ourselves of the whole body of scientific truth already accumulated, and when once we have obtained a probable hypothesis, we must not rest until we have verified it by comparison with new facts. * * * Out of the infinite number of observations and experiments which are possible at every moment, theory must lead us to select those few critical ones which are suitable for confirming or negating our anticipations."

A little later (p. 137) he remarks:

"The true course of inductive procedure is that which has yielded all the more lofty and successful results of science. It consists in anticipating Nature, in the sense of forming hypotheses as to the laws which are probably in operation; and then observing whether the combinations of phenomena are such as would follow from the laws supposed. The investigator begins with facts and ends with them. He uses such facts as are in the first place known to him in suggesting probable hypotheses; deducing other facts which would happen if a particular hypothesis is true, he proceeds to test the truth of his notion by fresh observations or experiments. If any result prove different from what he expects, it leads him either to abandon, or to modify his hypothesis; but every new fact may give some new suggestion as to the laws in action."

I may quote one more sentence from the Manchester logician (p. 138): "Agreement with fact is the one sole and sufficient test of a true hypothesis."

So I come with a general hypothesis of the evolution of living things, and of plants in particular. This hypothesis is based upon observed facts, which are here given such a uniform interpretation as will make my general hypothesis, and it is this latter that I wish to discuss to-day, making such application as will enable us to arrange the flowering plants in accordance with it.

I am going to confine my discussion pretty largely to the plants of the highest phylum, here restricted to those that bear flowers. Since the discovery of the pteridosperms, it is manifestly untenable to regard all seed-bearing plants as members of one phylum. In other words, the *Spermatophyta* of the books constitute not one phylum, but several phyla. Briefly, I shall exclude first of all the cycad phylum which began in the Paleozoic period with the pteridosperms, and has extended with many losses to the present. I shall also exclude the conifer phylum, related to but not included in the cycad phylum. These two phyla are commonly associated in a group under the name of gymnosperms, but I have no hesitation in keeping them as distinct phyla, the cycads lower, and the conifers higher.

The remaining seed-bearing plants, whose seeds are enclosed in carpels, constituting the old group of angiosperms, I regard as a distinct phylum, and because the flower is the dominant and characteristic structure, I designate them as the Phylum *Anthophyta*, and they are the flowering plants about which I speak to-day.

So in clearing the way for this discussion, let me show the relationship of these three phyla of higher plants by means of an analytic key, as follows:

- A. Gametophyte generation larger, and longer-lived than the dependent sporophyte generation. Here are set off the liverworts and mosses.
- B. Gametophyte generation smaller and shorter-lived than the independent sporophyte generation.
 - (a) Here we set off those plants in which both generations are mostly holophytic and independent of one another, the megagametophyte still containing chlorophyll, including ferns, calamites, and lycopods.

(b) Gametophytes hysterozytic, dependent upon, and nourished by, the sporophytes, the megagametophyte not containing chlorophyll.

(1) Megagametophyte a fully developed cellular mass before the formation of the eggs; microgametophytes few-celled; antherids basical; sperms ciliated and motile; megasporophylls open, in simple spirals to simple strobili; seeds fleshy; microsporophylls mostly multispangiate; bundles tracheidal, in a small, little-enlarging cylinder; pith and cortex large; stems simple; leaves ample, mostly pinnate, persistent, veins parallelCYCAD PHYLUM

(2) Megagametophyte a fully developed cellular mass before the formation of the eggs; microgametophytes few (to one)-celled; antherid apical; sperms non-ciliated and not visibly motile; megasporophylls open, in well-developed strobili; seeds not fleshy; microsporophylls with few (2-8) spangia; bundles tracheidal, in an enlarging cylinder; pith and cortex small; stems branched; leaves small, simple, persistent, veins parallelCONIFER PHYLUM

(3) Megagametophyte fully developed as a cellular mass (endosperm) only after the fertilization of the egg; microgametophytes one-celled; antherids apical; sperms non-ciliated and not visibly motile; megasporophylls closed (carpels), in floral strobili (flowers), often much reduced; seeds not fleshy; microsporophylls (stamens) with four spangia; bundles fibrovascular, in an enlarging cylinder; pith and cortex small (or bundles scattered and stem non-enlarging); stems branched; leaves mostly large, simple to compound, persistent to deciduous, veins netted to parallelFLOWERING PLANT PHYLUM

In the foregoing analysis, I have emphasized the similarities rather than the dissimilarities between the plants of these phyla, and such a statement will serve to show that they are related, and yet no one can compare them and not be forced to the conclusion that they must have diverged from one another at an early period in their evolution. And this divergence is to be interpreted as involving the cycad phylum as the primitive group from which have sprung the conifers on the one hand and the flowering plants on the other.

Following the plan which I adopted in my earlier paper,¹ I may here designate a number of generally accepted principles of classification as they apply to the flowering plants. While generally accepted, these principles have rarely if ever been formulated by taxonomists or others, so that as here formulated they may create some surprise and perhaps some opposition.

For the sake of brevity I give them in the form of dicta, as follows:

A. GENERAL DICTA

1. Evolution is not always upward, but often it involves degradation and degeneration.

¹ *Loc. cit.*

2. In general, homogeneous structures (with many and similar parts) are lower, and heterogeneous structures (with fewer and dissimilar parts) are higher.
3. Evolution does not necessarily involve all organs of the plant equally in any particular period, and one organ may be advancing while another is retrograding.
4. Upward development is sometimes through an increase in complexity, and sometimes by a simplification of an organ or a set of organs.
5. Evolution has generally been consistent, and when a particular progression or retrogression has set in, it is persisted in to the end of the phylum.
6. In any phylum the holophytic (chlorophyll-green) plants precede the colorless (hysterophytic) plants, and the latter are derived from the former.
7. Plant relationships are *up and down* the genetic lines, and these must constitute the framework of phylogenetic taxonomy.

B. DICTA HAVING SPECIAL REFERENCE TO THE GENERAL
STRUCTURE OF THE FLOWERING PLANTS

8. The stem structure with collateral vascular bundles arranged in a cylinder is more primitive than that with scattered bundles, and the latter are to be regarded as derived from the former.
9. Woody stems (as of trees) are more primitive than herbaceous stems, and herbs are held to have been derived from trees.
10. The simple, unbranched stem is an earlier type, from which branching stems have been derived.
11. Historically the arrangement of leaves in pairs on the stem is held to have preceded the spiral arrangement in which the leaves are solitary at the nodes.
12. Historically simple leaves preceded branched ("compound") leaves.
13. Historically leaves were first persistent ("evergreen") and later deciduous.
14. The reticulated venation of leaves is the normal structure,

and the parallel venation of some leaves is a special modification derived from it.

C. DICTA HAVING REFERENCE TO THE FLOWERS OF FLOWERING PLANTS

15. The polymeric flower structure precedes, and the oligomeric structure follows from it, and this is accompanied by a progressive sterilization of sporophylls.
16. Petaly is the normal perianth structure, and apetaly is the result of perianth reduction (aphanisis).
17. The apochlamydeous perianth is earlier and the gamochlamydeous perianth is derived from it by a symphysis of the members of perianth whorls.
18. Actinomorphy is an earlier structure than zygomorphy, and the latter results from a change from a similar to a dissimilar growth of the members of the perianth whorls.
19. Hypogyny is the more primitive structure, and from it epigyny was derived later.
20. Apocarpy is the primitive structure, and from it syncarpy was derived later.
21. Polycarpy is the earlier condition, and oligocarpy was derived from it later.
22. The endospermous seed is primitive and lower, while the seed without endosperm is derived and higher.
23. Consequently, the seed with a small embryo (in endosperm) is more primitive than the seed with a large embryo (in scanty or no endosperm).
24. In earlier (primitive) flowers there are many stamens (polystemonous) while in later flowers there are fewer stamens (oligostemonous).
25. The stamens of primitive flowers are separate (apostemonous), while those of derived flowers are often united (synstemonous).
26. The condition of powdery pollen is more primitive than that with coherent or massed pollen.
27. Flowers with both stamens and carpels (monoclinous) precede those in which these occur on separate flowers (diclinous).

28. In diclinous plants the monoecious condition is the earlier, and the dioecious later.

Let us now endeavor to apply these principles candidly in an attempt to secure a phyletic taxonomy of the flowering plants.

As a consequence, we begin with the plants that are primitively opposite-leaved, as shown by their first leaves ("cotyledons") that are always opposite. These are what we have known as dicotyledons. But this name, which was once significant, is no longer useful, and in fact has become somewhat misleading, so that I propose to substitute for it the name *Oppositifoliae* for the first class of the *Anthophyta*. Likewise for the other class, hitherto known as the monocotyledons, in which the leaves are alternate from the first, and continue so throughout the whole plant body, I propose the more appropriate name of *Alternifoliae*.

In considering these two classes, it is quite evident that the first is not only the larger in the number of its species, but also that it includes many more important modifications of structure than does the other. Yet there is much similarity in the kinds of modification of structure in the two classes, the larger class, from its very largeness, including many more details of modification and variation.

In both classes we begin with apocarpous plants, and proceed toward those that are syncarpous. So the *Ranales* on the one hand, and the *Alismatales* on the other, are near the point of beginning. In one class syncarpy is attained after the passing of a few hundred species (*Alismatales*, 409 species), while in the other it is not reached until much beyond the limits of the order *Ranales*, for it is well known that the syncarpy of many *Malvales* and *Geraniales* is distinctly incomplete, the coherence between the carpels being so feeble that they readily separate at maturity. All told, fully 10,000 species of this class are passed before complete syncarpy is attained.

The strobiloid flower structure, in which the axis is elongated, cylindrical, spheroidal, or flattened, bearing on its sur-

face the fertile and sterile sporophylls, prevails in the earlier orders of both classes, in the smaller, continuing through the *Alismatales*, *Liliales*, *Arales*, *Palmales*, and *Graminales*, and aggregating more than 11,700 species. In the larger class the strobiloid structure prevails throughout fourteen orders, from the *Ranales* to the *Lamiales*, and aggregating more than 53,000 species. In these strobiloid flowers, as a result of the dominance of the strobilar structure, we have what has been known as the hypogynous form of flower. In both classes the strobiloid flowers show progressive modifications involving the perianth (actinomorphy to zygomorphy, diploclamydy to achlamydy), the stamens (polystemony to oligostemonony), the carpels (polycarpy to oligocarpy), the ovules (multiovulate to rariovulate). In the larger class the perianth modifications proceed with such regularity that we may recognize lower (apopetalous), and higher (sympetalous) groups of orders, but this is not observed in the smaller class, where indeed sympetaly is never more than sporadic, and does not become a fixed structure.

In summary fashion I may now outline the taxonomy of the flowering plants:

The opposite-leaved class (*Oppositifoliae*, or dicotyledons) is the first to emerge from the cycadean phylum, appearing as the ranalean complex.

From this Ranalean type arises the alternate-leaved class of flowering plants (*Alternifoliae*, or monocotyledons) as apocarpous *Alismatales*, and these soon merge into the syncarpous *Liliales*, which are successively more and more modified in the *Arales*, *Palmales* and *Graminales*. From *Liliales* by a cotyloid modification the mostly actinomorphic epigynous *Iridales* are derived, and from these again the zygomorphic epigynous *Orchidales*.

Returning to the *Ranales*, we find that they give rise first to five apopetalous, polycarpellate orders with gradually increasing syncarpy, namely *Malvales*, *Geraniales*, *Guttiferales*, *Rhocadales*, and *Caryophyllales*. From the last arise three orders of sympetalous, polycarpellate plants, the *Ebenales*, *Ericales* and *Primulales*, and the latter have developed the

dicarpellate orders *Gentianales*, *Polemoniales*, *Scrophulariales* and *Lamiales*, constituting a series which shows diminishing numbers of stamens, carpels and seeds, and increasing zygomorphy. This phyletic sequence from *Ranales* to *Lamiales* constitutes the sub-class *Strobiloideae*, or cone-flowers.

Returning again to the *Ranales*, we find that they give rise to the simpler, cotyloid, apopetalous, polystemonous, polycarpous, hypogynous *Rosales* (sub-class *Cotyloideae*), from which by the early deepening of the cotyloid structure we have the mostly polystemonous, polycarpous, epigynous *Myrtales*, *Loasales* and *Cactales* as a strongly developed side line. The oligostemonous *Celastrales* continue the main phyletic line with reducing numbers of stamens, carpels and seeds, and a gradual deepening of the cup, to the side-line of the *Sapindales*, which are eventually epigynous, and the mostly dicarpellate *Umbellales*. The sympetalous, epigynous *Rubiales* with reduced calyx, few carpels and few seeds, pass easily into the *Campanulales*, and the *Asterales*, the latter with but one seed in the dicarpellary, one-celled, one-seeded, inferior ovary, and with its calyx, when not obsolete, transformed into bracts, spines or bristles to form a "pappus" for the efficient distribution of the seeds.

II. TAXONOMY OF FLOWERING PLANTS

Phylum XIV. **ANTHOPHYTA.** The Flowering Plants.

Typically chlorophyll-green plants (a few colorless hystero-phytes), ranging from small or even minute plants to great trees a hundred or more meters in height; alternation of generations obscured by the extreme reduction of the gametophyte to a condition of dependence upon the long-lived, leafy-stemmed sporophyte. Spores of two kinds (heterosporous), produced on sporophylls which are borne in modified, often much reduced strobili (flowers); microsporophylls (stamens) normally with four sporangia (pollen sacs); the microspores being set free (as "pollen") when mature; megasporophylls (carpels) folded lengthwise (constituting the "pistil") enclosing the sporangia (ovules) in which the megaspores

remain and develop the minute gametophyte; archegones very much reduced, including little more than the egg, which is

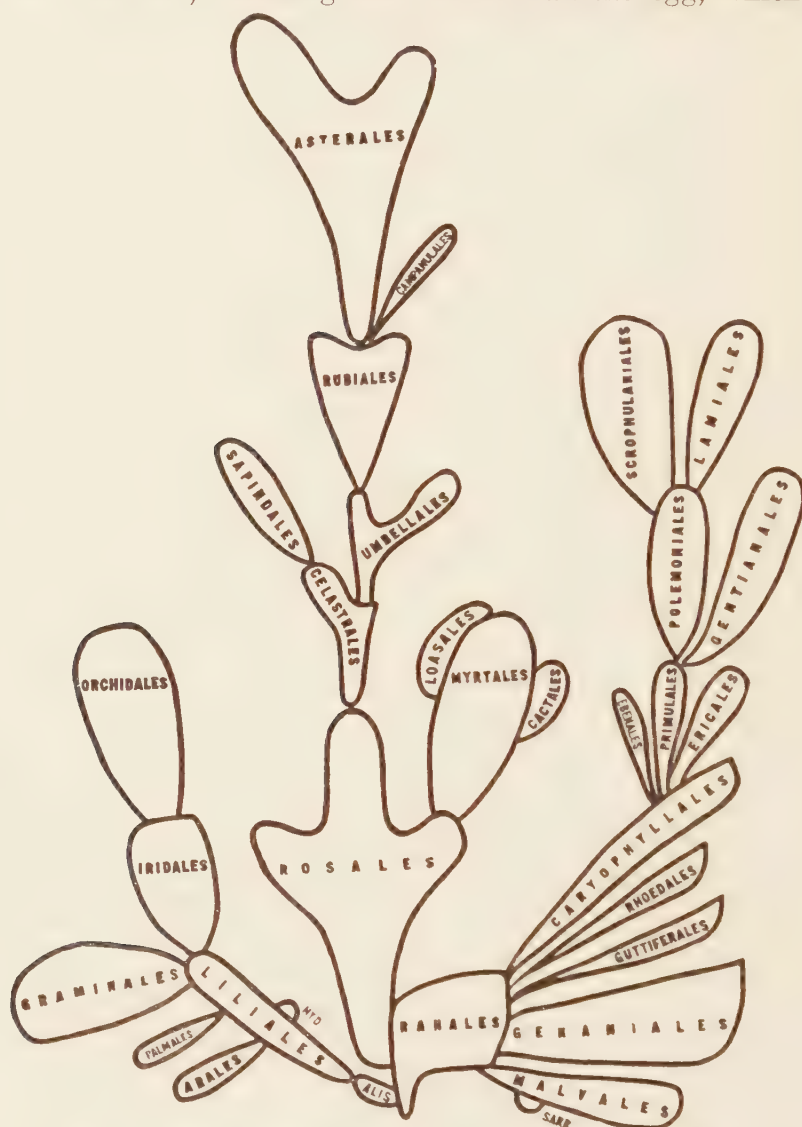


Fig. 1. Chart to show relationship of the orders. Relationship is indicated by position; the areas are approximately proportional to the number of species in the orders.

fecundated by the non-ciliated sperms (male nuclei) from the tubular antherids, resulting in the formation of an embryo

sporophyte; megasporangia surrounded by one or two enveloping indusial coats (seed coats); mature seed with or without endosperm (gametophyte tissue).

The flowering plants are here held to have sprung from cycadean strobiliferous ancestors, probably of the general type of the *Bennettitineae*, and as a consequence those anthophyta are considered to be primitive in which the sporophylls are many and distinct. Symphyllly and syncarpy are later structural conditions than apophyllly and apocarpy. So also, fewer sporophylls in the anthostrobilus is a later condition derived from the earlier polyphyllous structure. The symphysis of sporophylls is a mode of evolution, and so is their aphanisis.

The plants constituting this phylum are those commonly termed angiosperms, in contrast with the gymnosperms, including the cycads (*Cycadophyta*) and conifers (*Strobilophyta*). It appears to the writer, however, that these are more properly three pretty distinct phyla, and that the relationship of the gymnosperms to the angiosperms is so remote that the treatment here given them is more nearly in accordance with what is known as to their phylogeny.

There are two classes, *Alternifoliae* (monocotyledons) and *Oppositifoliae* (dicotyledons), of which the second was quite certainly the earlier, as it is now much the larger numerically. Indeed, it is becoming more probable that the monocotyledons are to be regarded as a peculiar side branch which sprang from the primitive dicotyledons after the latter had become well established. Yet the monocotyledons have not developed to as high a rank in any of their orders as have some of the dicotyledons.

Although I have here changed the technical names of these two classes, there is no objection to the retention of the old terms for the English names in popular usage: accordingly on the following pages I shall frequently make such use of the old names.

Class 32. ALTERNIFOLIAE (MONOCOTYLEDON-EAE). The Monocotyledons. Leaves of young sporophyte

alternate; leaves of mature sporophyte alternate, and usually parallel-veined; fibro-vascular bundles of the stem scattered, usually not arranged in rings. (Species about 23,700.)

Sub-Class **ALTERNIFOLIAE-STROBILOIDEAE**. Axis of the flower from spheroidal to flattened, bearing on its surface the hypogynous perianth and stamens (or the stamens may be attached to the perianth), and the many or few, superior, separate or united carpels.

Order **ALISMATALES**. Carpels separate, superior to all other parts of the flower; endosperm scanty or none (species about 409). Related to and probably derived from the *Ranales* of the dicotyledons.

Family 1. **Alismataceae**. Water Plantains. Aquatic or paludose herbs with mostly radical, often large leaves; flowers small to large; perianth in two whorls of three leaves each (calyx and corolla); placenta sutural; ovules mostly solitary. *Alisma*, *Sagittaria*. (Pf. 2¹: 227.)¹

Family 2. **Butomaceae**. Aquatic or paludose herbs, bearing narrow or broad leaves, with convergent veins; flowers large; perianth in two whorls, of three leaves each (calyx and corolla); placenta parietal; ovules many. *Butomus*, *Limncharis*. (Pf. 2¹: 232.)

Family 3. **Triuridaceae**. Very small, pale, leafless plants growing in wet places in tropical countries. *Triuris*. (Pf. 2¹: 235.)

Family 4. **Scheuchzeriaceae**. Aquatic or paludose herbs with rush-like leaves, and small flowers, with a two-whorled perianth, each 4-6-parted. *Triglochin*, *Scheuchzeria*. (Pf. 2¹: 222.)

Family 5. **Typhaceae**. Cat-tails. Aquatic or paludose herbs, with linear, sheathing leaves and cylindrical-crowded flowers; pistil 1-celled; ovule 1. *Typha*. (Pf. 2¹: 183.)

Family 6. **Sparganiaceae**. Aquatic or paludose plants with creeping rootstocks and erect stems, bearing linear

¹ The abbreviation "Pf." has reference to Engler and Prantl's 'Natürlichen Pflanzenfamilien,' and the bold face, exponent, and Roman figures following refer respectively to "Abteilung," "Teil," and page of this publication.

leaves; flowers monoecious in dense globose heads. *Sparanium*. (Pf. 2¹:192.)

Family 7. **Pandanaceae**. Screw-pines. Shrubs or trees with spirally crowded, narrow, stiff leaves on the ends of the branches; pistil 1-celled; ovules one or many. *Pandanus*. (Pf. 2¹:186.)

Family 8. **Aponogetonaceae**. Aquatic plants with petioled, oblong, translucent leaves, with convergent veins; flowers small, spicate. *Aponogeton*. (Pf. 2¹:218.)

Family 9. **Potamogetonaceae**. River-weeds. Aquatic or paludose herbs with mostly alternate stem-leaves; flowers mostly small and inconspicuous; perianth none, or of 1-6 leaves in 1 or 2 whorls. *Potamogeton*, *Zostera*, *Zannichellia*. (Pf. 2¹:194.)

Order LILIALES. Carpels united (usually 3), forming a compound pistil, superior; perianth (usually of 6 parts) in two similar whorls, delicate and corolla-like; endosperm copious. (Species about 3370.)

Family 10. **Liliaceae**. The Lilies. Pistil mostly 3-celled; stamens 6; perianth of two similar whorls, each of three similar leaves. *Lilium*, *Erythronium*, *Tulipa*, *Yucca*, *Asparagus*, *Allium*. (Pf. 2⁵:10.)

Family 11. **Stemonaceae**. Pistil 1-celled; stamens 4; perianth of two similar whorls, each of two similar leaves. *Stemona*, *Croomia*. (Pf. 2⁵:8.)

Family 12. **Pontederiaceae**. Aquatic herbs with 3 or 1-celled pistil; stamens 6 or 3; perianth of two similar whorls, each of three similar or dissimilar leaves. *Pontederia*, *Heteranthera*. (Pf. 2⁴:70.)

Family 13. **Cyanastraceae**. Tropical African rhizomatous plants. *Cyanastrum*. (Syllabus, 141.)¹

Family 14. **Philydraceae**. Pistil 3-celled; stamen 1; perianth of two similar whorls, each of two dissimilar leaves. *Philydrium*. (Pf. 2⁴:75.)

¹ "Syllabus" has reference to Engler and Gilg's 'Syllabus der Pflanzenfamilien,' and the numbers following refer to pages of this publication.

Family 15. **Commelinaceae**. Spiderworts. Succulent herbs with 3 or 2-celled pistil; stamens 6; perianth of two dissimilar whorls of three similar leaves. *Commelina*, *Tradescantia*. (Pf. 2⁴: 60.)

Family 16. **Xyridaceae**. Rush-like plants with a 1-celled or incompletely 3-celled pistil; stamens 3; perianth of two dissimilar whorls, each of three similar leaves. *Xyris*. (Pf. 2⁴: 18.)

Family 17. **Mayacaceae**. Slender, creeping, moss-like plants with 1-celled pistil; stamens 3; perianth of two dissimilar whorls, each of three similar leaves. *Mayaca*. (Pf. 2⁴: 16.)

Family 18. **Juncaceae**. Rushes. Herbs with narrow leaves; pistil 1-3-celled; ovules solitary or many; fruit a dry 3-valved pod. *Juncus*, *Luzula*. (Pf. 2⁵: 1.)

Family 19. **Eriocaulonaceae**. Rush-like herbs with flowers in close heads; perianth segments 6 or less, small; pistil 3 or 2-celled; ovules orthotropous, pendulous. *Eriocaulon*. (Pf. 2⁴: 21.)

Family 20. **Thurniaceae**. South American herbs, with small, 1-nerved leaves, and small axillary flowers. *Thurnia*. (Syllabus, 139.)

Family 21. **Rapateaceae**. Tall, sedge-like marsh herbs with 3-celled pistil; stamens 6, in pairs; perianth of two dissimilar whorls, each of three similar leaves. *Rapatea*. (Pf. 2⁴: 28.)

Family 22. **Naiadaceae**. Slender, branching, wholly submerged aquatics, with sheathing, mostly opposite leaves, and monoecious or dioecious flowers. *Naias*. (Pf. 2¹: 214.)

Order ARALES. Compound pistil, mostly tricarpellary, superior; ovules one or more; perianth reduced to scales or entirely wanting; endosperm usually present. (Species about 1052.)

Family 23. **Cyclanthaceae**. Mostly herbaceous plants with broad, petioled leaves having parallel venation; pistil 1-celled; ovules many, on four parietal placentae. *Cyclanthus*. (Pf. 2³: 93.)

Family 24. **Araceae**. Arums. Mostly herbaceous plants with broad, petioled leaves, having reticulate venation; pistil 1-4-celled; ovules 1 or more. *Anthurium*, *Acorus*, *Monstera*, *Symplocarpus*, *Calla*, *Philodendron*, *Calocasias*, *Caladium*, *Arum*, *Arisaema*. (Pf. 2³:102.)

Family 25. **Lemnaceae**. Duckweeds. Very small, floating, aquatic herbs; pistil 1-celled; ovules 1 or more. *Lemna*, *Spirodela*. (Pf. 2³:154.)

Order PALMALES. Compound pistil mostly tricarpellary, superior; ovule solitary; perianth reduced to rigid or herbaceous scales; endosperm copious. (Species about 1085.)

Family 26. **Palmaceae**. Palms. Trees or shrubs with pinnate or palmate leaves; pistil 1-3-celled; fruit a 1-seeded berry or drupe (rarely 2-3-seeded). *Phoenix*, *Chamaerops*, *Calamus*, *Oreodoxa*, *Cocos*. (Pf. 2³:1.)

Order GRAMINALES. Compound pistil reduced to 2 or 3 carpels; ovule solitary; perianth reduced to small scales or entirely wanting; endosperm copious. (Species about 5795.)

Family 27. **Restionaceae**. Rush-like herbs or undershrubs, with spiked, racemed, or paniced mostly diclinous flowers; perianth segments 6 or less, chaffy; pistil 1-3-celled; ovules orthotropous, pendulous. *Restio*. (Pf. 2⁴:3.)

Family 28. **Centrolepidiaceae**. Small rush-like herbs with mostly monoclinal flowers in spikes or heads; perianth none; pistil 1-several-celled; ovules orthotropous, pendulous. *Centrolepis*. (Pf. 2⁴:11.)

Family 29. **Flagellariaceae**. Erect or climbing herbs with long narrow leaves, and paniced flowers; pistil 3-celled; ovules solitary, anatropous, ascending; fruit a 1-2-seeded berry. *Flagellaria*. (Pf. 2⁴:1.)

Family 30. **Cyperaceae**. Sedges. Grass-like herbs with 3-ranked leaves; perianth segments bristly or none; pistil 1-celled; ovules anatropous, erect. *Cyperus*, *Scirpus*, *Fimbristylis*, *Rhynchospora*, *Carex*. (Species 1959.) (Pf. 2²:98.)

Family 31. **Poaceae**. Grasses. Mostly erect herbs with hollow, jointed stems, and 2-ranked leaves; perianth segments

of 2-6 scales or vestiges; pistil 1-celled; ovules anatropous, ascending. *Bambusa*, *Bromus*, *Triticum*, *Bouteloua*, *Avena*, *Agrostis*, *Phalaris*, *Oryza*, *Panicum*, *Andropogon*, *Zea*. (Species 3545.) (Pf. 2²:1.)

In the *Poaceae* the hypogynous, tricarPELLARY monocOTYLEDONS reach their culmination, as a highly specialized side line. In grasses the specialization involves plant-body, inflorescence, and flowers. Their nodose, mostly hollow, elongated stems, and long, narrow, tough leaves; the spreading paniculate arrangement of their spikelets; and their 1-celled, tricarPELLARY 1-ovuled pistils, producing caryopsis-fruits, are some of the more obvious indications of high specialization, suggesting the possibility that these plants, rather than the orchids, are the highest of the monocOTYLEDONS. With the *Poaceae* the hypogynous monocOTYLEDONOUS phylum ends. Grasses have not given rise to other groups of plants.

Sub-Class ALTERNIFOLIAE - COTYLOIDEAE. Axis of the flower normally expanded into a cup, bearing on its margin the perianth and stamens (or the latter may be attached to the perianth). The carpels are thus inferior. Flowers from actinomorphic to zygomorphic.

Order HYDRALES. Flowers diclinous; compound tricarPELLARY pistil inferior to all other parts of the flower; perianth segments in each whorl alike in shape (flower regular); seeds without endosperm. (Species about 53.)

Family 32. **Vallisneriaceae**. Tape-grasses. Small aquatic herbs mostly inhabiting the fresh waters of temperate climates. *Vallisneria*, *Hydrocharis*, *Philotria*. (Pf. 2¹:238.)

Order IRIDALES. Compound tricarPELLARY pistil inferior; flower-leaves in each whorl mostly alike in shape (flower regular, actinomorphic); seeds with endosperm. (Species about 4419.)

Family 33. **Amaryllidaceae**. Amaryllises. Leaves narrow, or the blade broad, with longitudinal veins; pistil 3-celled; ovules many; stamens 6 or 3. *Amaryllis*, *Crinum*, *Narcissus*, *Agave*, *Hypoxis*. (Pf. 2⁵:97.)

Family 34. **Haemodoraceae**. Leaves sword-shaped; pistil 3-celled; ovules 1 to many; stamens 6. *Haemodorum*. (Pf. 2⁵:92.)

Family 35. **Iridaceae**. Leaves sword-shaped; pistil 3-celled; ovules many; stamens 3. *Crocus*, *Iris*, *Tigridia*, *Sisyrinchium*, *Ixia*, *Tritonia*, *Gladiolus*, *Freesia*. (Pf. 2⁵:137.)

Family 36. **Velloziaceae**. Woody-stemmed, leafy plants, with a 3-celled pistil containing many ovules, stamens 6 or more. *Vellozia*. (Pf. 2⁵:125.)

Family 37. **Taccaceae**. Stemless herbs, with broad pinnately parallel-veined leaves; pistil 1-celled; ovules many; stamens 6. *Tacca*. (Pf. 2⁵:127.)

Family 38. **Dioscoreaceae**. Yams. Mostly twining herbs, with broad, petioled, longitudinally-veined leaves; pistil 3-celled; ovules 2 in each cell; stamens 6. *Dioscorea*, *Testudinaria*. (Pf. 2⁵:130.)

Family 39. **Bromeliaceae**. Pineapples. Leaves mostly rosulate; external perianth whorl calycine; pistil 3-celled; ovules many; stamens 6. *Tillandsia*, *Dendropogon*, *Ananas*. (Pf. 2⁴:32.)

Family 40. **Musaceae**. Bananas. Large herbs, the stem often composed of the sheathing leaf-bases; perianth petaloid of 6, often dissimilar segments; stamens 6; pistil 3-celled; ovules 1 to very many. *Strelitzia*, *Musa*. (Pf. 2⁶:1.)

Family 41. **Zingiberaceae**. Ginger. Perennial, medium-sized herbs, with creeping or tuberous rootstocks; perianth irregular; stamen 1, anther 2-celled, with several "staminodes"; pistil 3-celled; ovules 1 or more in each cell. *Curcuma*, *Zingiber*, *Amomum*. (Pf. 2⁶:10.)

Family 42. **Cannaceae**. Cannas. Perennial herbs of medium size, with simple pinnately-veined leaves; perianth irregular; stamen 1, anther 1-celled, with several "staminodes"; pistil 3-celled; ovules 1 to many. *Canna*. (Pf. 2⁶:30.)

Family 43. **Marantaceae**. Perennial herbs of variable habit; leaves parallel or pinnately veined; perianth irregular; functional stamen 1, with several "staminodes"; pistil 3-

celled; ovules 1 in each cell. *Calathea*, *Maranta*. (Pf. 2⁶:33.)

Order ORCHIDALES. Compound tricarPELLARY pistil inferior; flower-leaves in each whorl mostly unlike in shape (flower irregular, zygomorphic); seeds numerous, minute, without endosperm. (Species about 7578.)

Family 44. **Burmanniaceae**. Flowers irregular; stamens 3 or 6. *Burmannia*. (Pf. 2⁶:44.)

Family 45. **Orchidaceae**. Orchids. Flowers irregular; stamens 1 or 2. *Cypripedium*, *Orchis*, *Platanthera*, *Vanilla*, *Spiranthes*, *Epidendrum*, *Dendrobium*, *Oncidium*. (Species 7521.) (Pf. 2⁶:52.)

In the *Orchidales*, and especially in the *Orchidaceae*, we have what is generally regarded as the highest development of monocotyledonous plants, and yet it must be acknowledged that many of their most striking flower structures are rather easily made entomophilous modifications of the perianth, the most mobile portion of the plant. In many ways the "grassy" plants (especially the *Poaceae*) show greater and more profound structural modifications than do the much more conspicuous orchids. With the orchids the epigynous monocotyledonous phylum ends.

Class 33. **OPPOSITIFOLIAE (DICOTYLEDONEAE)**. The Dicotyledons. Leaves of young sporophyte opposite; leaves of mature sporophyte opposite or alternate, usually reticulate-veined; fibrovascular bundles of the stem in one or more cylindrical layers. (Species about 108,800.)

As indicated above the dicotyledons are here considered to have had their beginning earlier than the monocotyledons, which must be regarded as having diverged very early from the primitive dicotyledons, and developed into a relatively small lateral branch. The point of divergence of the monocotyledons from the dicotyledons must have been in the order *Ranales*, probably in the neighborhood of the *Ranunculaceae*. It is not probable that the early (woody) magnoliads or anonads gave rise to the monocotyledonous divergence; it is much more probable that this modification arose after the reduction had taken place from the ligneous to the herbaceous *Ranales*.

Here we have a possible explanation of the marked herbaceousness of monocotyledons as contrasted with the general tendency toward a more ligneous structure in dicotyledons.

Sub - Class OPPOSITIFOLIAE - STROBILOIDEAE.
“Cone flowers.” Axis of the flower normally cylindrical, spherical, hemispherical or flattened, bearing on its surface the hypogynous perianth, stamens and pistils (or the stamens may be attached to the corolla).

Super - Order STROBILOIDEAE-APOPETALAE-POLYCARPELLATAE.
Carpels typically many, separate or united; petals separate. Flowers mostly actinomorphic. This super-order has much in common with the *Alismatales*, and also with the *Cotyledoneae-Apometalae*. In fact, these three groups appear to have diverged from a common point of origin.

Order RANALES. All parts of the flower mostly spirally arranged (acyclic), free (not united); carpels typically many, separate (or rarely united), rarely reduced to 1; stamens generally indefinite; embryo mostly small, in copious endosperm. (Species about 5551.)

The twenty-four families here included in the order *Ranales* naturally group themselves about three centers, the magnolias (*Magnoliaceae*), the anonas (*Anonaceae*), and the buttercups (*Ranunculaceae*). The plants in these centers are typically diplochlamydeous, polycarpellate, hermaphrodite, and actinomorphic, and the modifications in the surrounding families have been such as to result in an achlamydeous structure, which may be monocarpellate, diclinous, and even zygomorphic. Ranalean evolution has thus been one of more and more marked simplification of flower structure.

It is interesting to observe that while the families of *Ranales* have thus been evolved, the order has given rise to no less than five phyletic groups of full ordinal rank. One of these (*Malvales*) has produced a further modification (*Sarraceniales*), for three of them the evolutionary development came to a stand-still with the ordinal limits (*Geraniales*, *Guttiferales* and *Rhoedales*), while the virile *Caryophyllales* continued a development beyond its ordinal limits into the *Ebenales*, *Eri-*

cales and *Primulales*, and through the latter into *Gentianales*, *Polemoniales* and *Scrophulariales* to the end of this phyletic line in the *Lamiales*.

Family 46. **Magnoliaceae.** Magnolias. Petals present, usually many; receptacle usually elongated; shrubs and trees with alternate leaves and usually large flowers. *Magnolia*, *Liriodendron*. (Pf. 3²: 12.)

Family 47. **Calycanthaceae.** Petals present, usually many; seeds without endosperm; shrubs with opposite leaves. *Calycanthus*. (Pf. 3²: 92.)

Family 48. **Monimiaceae.** Petals absent; carpels many, 1-ovuled, embedded in the receptacle; trees and shrubs with opposite or whorled leaves, and diclinous flowers. *Kibara*, *Monimia*, *Siparuna*. (Pf. 3²: 94.)

Family 49. **Cercidiphyllaceae.** Trees with naked dioecious flowers, many stamens, and a single whorl of 2-5 free carpels. *Cercidiphyllum*. (Pf. 3²: 21.)

Family 50. **Trochodendraceae.** Trees and shrubs with naked flowers, many stamens, and a single whorl of 5 to many partly connate carpels. *Trochodendron*. (Pf. 3²: 21.)

Family 51. **Leitneriaceae.** Shrubs with alternate leaves and dioecious flowers in catkins; perianth minute or 0; pistil 1-celled, 1-ovuled; endosperm minute. *Leitneria*. (Pf. 3¹: 28.)

Family 52. **Anonaceae.** Papaws. Petals present, in two whorls of 3 each; stamens and carpels many; endosperm ruminated; trees or shrubs with alternate leaves. *Asimina*, *Anona*. (Pf. 3²: 23.)

Family 53. **Lactoridaceae.** Much-branched shrubs of the South Pacific Islands, with alternate leaves, and apetalous flowers. *Lactoris*. (Pf. 3²: 19.)

Family 54. **Gomortegaceae.** Large trees of South America, with opposite evergreen leaves, and acyclic flowers; carpels 2-3, each with 1 ovule. *Gomortega*. (Pf. Nachträge zu Teil II-IV, 172.)

Family 55. **Myristicaceae.** Nutmegs. Sepals 3; petals absent; pistil 1 (or a second rudiment), 1-seeded; endosperm

ruminated; trees or shrubs with alternate leaves and small, inconspicuous, dioecious flowers. *Myristica*. (Pf. 3²:40.)

Family 56. **Saururaceae**. Rhizomatous marsh herbs, with alternate leaves; flowers perfect, small, spicate; perianth 0; carpels 3–4, more or less united. *Saururus*. (Pf. 3¹:1.)

Family 57. **Piperaceae**. Peppers. Herbs, shrubs, and trees with alternate (or opposite) leaves; flowers perfect or diclinous, mostly spicate; perianth 0; pistil 1-celled, 1-ovuled; endosperm present. *Piper*, *Macropiper*. (Pf. 3¹:3.)

Family 58. **Lacistemaceae**. Tropical American shrubs and trees with alternate leaves, and perfect flowers; perianth mostly 0; stamen 1; pistil 3 or 2-carpellary. *Lacistema*. (Pf. 3¹:14.)

Family 59. **Chloranthaceae**. No perianth whatever; pistil 1, with 1 ovule; mostly tropical trees and shrubs, with opposite leaves, and small flowers. *Chloranthus*. (Pf. 3¹:12.)

Family 60. **Ranunculaceae**. Buttercups. Petals present in one whorl, or absent; sepals mostly deciduous; stamens and carpels indefinite, the latter usually separate; mostly herbs with alternate leaves. *Myosurus*, *Ranunculus*, *Anemone*, *Clematis*. (Pf. 3²:43.)

Family 61. **Lardizabalaceae**. Petals and sepals 6 each; stamens 6; twining or erect shrubs, with alternate leaves. *Akebia*, *Lardizabala*. (Pf. 3²:67.)

Family 62. **Berberidaceae**. Barberries. Petals usually present, in 1–3 whorls; stamens few; carpel 1 (rarely more), with many ovules; mostly shrubs with alternate leaves and perfect flowers. *Podophyllum*, *Berberis*. (Pf. 3²:70.)

Family 63. **Menispermaceae**. Moonseeds. Petals present, in 2 whorls; carpels 3 or more; twining shrubs with alternate leaves and small dioecious flowers. *Menispermum*, *Cocculus*. (Pf. 3²:78.)

Family 64. **Lauraceae**. Laurels. Aromatic trees and shrubs with alternate simple leaves and small flowers; petals 0; carpel 1; ovule 1, pendulous; endosperm 0. *Cinnamomum*, *Persea*, *Ocotea*, *Umbellularia*, *Sassafras*, *Litsea*, *Laurus*. (Pf. 3²:106.)

Family 65. **Nelumbaceae**. Lotuses. Large aquatic herbs with peltate leaves, large acyclic flowers, with many stamens, and many separate carpels, the latter immersed in the flattish axis ("receptacle"); seeds 1 or 2, endosperm 0. *Nelumbo*. (Pf. 3²: 1.)

Family 66. **Cabombaceae**. Water-shields. Small aquatic herbs with floating, sometimes peltate leaves, and few to many stamens, and separate carpels (not immersed); seeds 2 or 3; endosperm present. *Cabomba*, *Brasenia*. (Pf. 3²: 2.)

Family 67. **Ceratophyllaceae**. Aquatic herbs with verticillate, divided leaves; flowers diclinous; perianth 0; stamens 12-16; carpel 1, 1-ovuled; endosperm scanty. *Ceratophyllum*. (Pf. 3²: 10.)

Family 68. **Dilleniaceae**. Petals present, in one whorl; sepals persistent; stamens numerous, indefinite; carpels from many to 1, with 1 or more seeds; endosperm copious; mostly shrubs and trees with alternate leaves, and perfect flowers. *Dillenia*, *Actinidia*. (Pf. 3⁶: 100.)

Family 69. **Winteranaceae**. Aromatic trees with alternate leaves; flowers perfect; sepals 4-5; petals 4-5 (or 0); stamens 20-30; pistil 2-5-carpellary, with as many parietal placentae; endosperm copious. *Winterana*, *Cinnamodendron*. (Pf. 3⁶: 314.)

Order MALVALES. Pistil usually of 3 to many weakly united carpels, with as many cells (sometimes greatly reduced); ovules mostly few; stamens indefinite, monadelphous, branched, or by reduction separate and few; endosperm present or absent. (Species about 3829.)

Family 70. **Sterculiaceae**. Trees and shrubs with alternate leaves; flowers perfect or diclinous, with or without petals; stamens monadelphous or polyadelphous, 2-celled; pistil 4-many-celled; endosperm present or 0. *Theobroma*, *Sterculia*. (Pf. 3⁶: 69.)

Family 71. **Malvaceae**. Mallows. Herbs, shrubs, and trees with alternate leaves; flowers perfect, with petals; stamens monadelphous, 1-celled; pistil 5-many-celled; endosperm little

or 0. *Abutilon*, *Althaea*, *Malva*, *Hibiscus*, *Gossypium*. (Pf. 3⁶:30.)

Family 72. **Bombacaceae**. Tropical trees with alternate, palmate leaves; sepals and petals present; staminal column 5–8-cleft. *Adansonia*, *Bombax*. (Pf. 3⁶:53.)

Family 73. **Scytopetalaceae**. Trees of the southern hemisphere, with alternate leathery leaves; sepals small; petals much larger, valvate; stamens many. *Scytopetalum*. (Pf. Nachträge zu Teil II–IV, 242.)

Family 74. **Chlaenaceae**. Madagascar trees and shrubs with alternate leaves; inflorescence dichotomous; petals contorted. *Rhodochlaena*, *Leptochlaena*. (Pf. 3⁶:168.)

Family 75. **Gonystylaceae**. East Indian trees with leathery, evergreen leaves, pentamerous flowers, and a berry-like fruit. *Gonystylus*. (Pf. Nachträge zu Teil II–IV, 231.)

Family 76. **Tiliaceae**. Lindens. Trees, shrubs (and herbs) with mostly alternate leaves; flowers mostly perfect, with petals; stamens free, 2-celled; pistil 2–10-celled; endosperm present or 0. *Corchorus*, *Tilia*, *Grewia*. (Pf. 3⁶:8.)

Family 77. **Elaeocarpaceae**. Tropical trees and shrubs, with alternate or opposite simple leaves; sepals and petals present; stamens distinct, many; pistil of 2–several carpels. *Elaeocarpus*, *Aristotelia*. (Pf. 3⁶:1.)

Family 78. **Balanopsidaceae**. Australian trees and shrubs with alternate leaves; flowers dioecious, apetalous, the staminate in catkins, the pistillate solitary, producing acorn-like, 2-celled, 2-seeded fruits; seeds endospermous. This family is doubtfully given place here, and it may be that it should be placed near the *Fagaceae*, as is done by Baillon. *Balanops*. (Pf. Nachträge zu Teil II–IV, 114.)

Family 79. **Ulmaceae**. Elms. Trees and shrubs with alternate, simple leaves, small apetalous flowers, a 1-celled (rarely 2-celled) ovary, which develops into a samara, drupe or nut. *Ulmus*, *Celtis*, *Zelkova*, *Planera*. (Pf. 3¹:59.)

Family 80. **Moraceae**. Figs. Trees, shrubs, and herbs, mostly with a milky juice, and alternate or opposite leaves;

flowers apetalous, diclinous (monoecious or dioecious); ovary 1-celled, 1-ovuled. *Morus*, *Toxylon* (*Maclura*), *Broussonetia*, *Dorstenia*, *Artocarpus*, *Castilloa*, *Antiaris*, *Ficus*, *Humulus*, *Cannabis*. (Pf. 3¹:66.)

Family 81. **Urticaceae**. Nettles. Herbs, shrubs, and trees with alternate or opposite leaves; flowers mostly diclinous, apetalous; stamens few, 2-celled; pistil monocarpellary, 1-celled, mostly 1-seeded; endosperm none. *Urtica*, *Boehmeria*. (Pf. 3¹:98.)

Order SARRACENIALES. Pistil of 3-5 carpels united; placentae parietal or central; seeds small, numerous, endospermous; herbs with "insectivorous" leaves; related to the mallows, with which they should possibly be included. (Species about 66.)

Family 82. **Sarraceniaceae**. Pitcher-plants. Herbs with pitcher-shaped leaves, and perfect flowers; sepals 4-5; petals 5, rarely 0; stamens indefinite; pistil 3-5-carpellary. *Sarracenia*, *Darlingtonia*. (Pf. 3²:244.)

Family 83. **Nepenthaceae**. Pitcher-plants. Tropical undershrubs with pitcher-shaped leaves and dioecious flowers; sepals 4 or 3; petals 0; stamens 4-16; pistil 4-3-carpellary. *Nepenthes*. (Pf. 3²:253.)

Order GERANIALES. Pistil of several (5-2) mostly weakly united carpels; ovules 1-2 (or many), mostly pendulous, attached at the inner angle of the carpel. (Species about 9268.)

Family 84. **Geraniaceae**. Geraniums. Herbs, shrubs, and trees, with opposite or alternate (compound or simple) leaves; torus elongated; stamens 10; pistil mostly 5-celled; ovules few; endosperm sparse or 0. *Geranium*, *Pelargonium*, *Erodium*. (Pf. 3⁴:1.)

Family 85. **Oxalidaceae**. Sorrels. Herbs, rarely shrubs or trees, the juice sour; leaves mostly 3 or more foliate; flowers pentamerous, regular; stamens 10; ovules many; endosperm fleshy. *Oxalis*. (Pf. 3⁴:15.)

Family 86. **Tropaeolaceae**. Nasturtiums. Succulent, prostrate or climbing herbs, with alternate, peltate leaves, and

irregular, long-peduncled, spurred flowers; stamens 8; ovary tricarpellary; ovules solitary; endosperm 0. *Tropaeolum*. (Pf. 3⁴: 23.)

Family 87. **Balsaminaceae**. Touch-me-nots. Succulent herbs, mostly erect, with opposite or alternate leaves, and irregular, spurred axillary flowers; stamens 5; ovary pentacarpellary, ovules many; endosperm 0. *Impatiens*. (Pf. 3⁵: 383.)

Family 88. **Limnanthaceae**. Succulent marsh herbs, with alternate, pinnate leaves; flowers pentamerous; stamens 10; carpels 5; endosperm 0. *Limnanthes*. (Pf. 3⁵: 136.)

Family 89. **Linaceae**. Flaxes. Herbs and shrubs, with alternate simple leaves; pistil 3-5-celled; endosperm fleshy (or rarely 0). *Linum*. (Pf. 3⁴: 27.)

Family 90. **Humiriaceae**. Trees with alternate simple leaves; pistil 5-7-celled; endosperm copious. *Humiria*, *Sacoglottis*. (Pf. 3⁴: 35.)

Family 91. **Erythroxylaceae**. Shrubs and trees, with mostly alternate, simple leaves; flowers pentamerous; stamens 10; ovary 3-4-carpellary; fruit a drupe; endosperm fleshy. *Erythroxylon*. (Pf. 3⁴: 37.)

Family 92. **Zygophyllaceae**. Herbs and shrubs with usually opposite, compound leaves; pistil lobed, 4-5-celled; endosperm copious (or rarely 0). *Zygophyllum*, *Guaiacum*, *Larrea*. (Pf. 3⁴: 74.)

Family 93. **Cneoraceae**. Shrubs with alternate entire leaves, trimerous or tetramerous flowers; pistil 3 or 4-celled, each cell with one ovule; endosperm fleshy. *Cneorum*. (Pf. 3⁴: 93.)

Family 94. **Rutaceae**. Oranges. Herbs, shrubs, and trees with glandular-dotted, opposite, simple, or compound leaves; pistil lobed, 4-5-celled; endosperm fleshy or 0. *Xanthoxylum*, *Ruta*, *Dictamnus*, *Ptelea*, *Limonia*, *Citrus*. (Pf. 3⁴: 95.)

Family 95. **Simarubaceae**. Trees and shrubs with generally alternate, non-glandular, simple, or compound leaves; pistil lobed, 1-5-celled; endosperm fleshy or 0. *Simaruba*, *Quassia*, *Holacantha*, *Ailanthus*. (Pf. 3⁴: 202.)

Family 96. **Burseraceae.** Balsamic trees and shrubs with alternate compound leaves; pistil 2-5-celled; endosperm 0. *Protium*, *Canarium*, *Bursera*. (Pf. 3⁴: 231.)

Family 97. **Meliaceae.** Trees and shrubs with alternate compound leaves; pistil 3-5-celled; endosperm present or 0. *Swietenia*, *Melia*. (Pf. 3⁴: 258.)

Family 98. **Malpighiaceae.** Trees and shrubs with usually opposite, simple or lobed leaves; pistil tricarpestry; endosperm 0. *Stigmatophyllon*, *Malpighia*, *Byrsonima*. (Pf. 3⁴: 41.)

Family 99. **Trigoniaceae.** Climbing shrubs with opposite simple leaves and irregular flowers; pistil tricarpestry; seeds many, endospermous. *Trigonia*. (Pf. 3⁴: 309.)

Family 100. **Vochysiaceae.** Shrubs and trees with opposite or whorled leaves; sepals 5; petals 1, 3, or 5; stamens several, usually but one fertile; pistil tricarpestry; seeds few; endosperm 0. *Vochysia*, *Qualea*. (Pf. 3⁴: 312.)

Family 101. **Polygalaceae.** Herbs, shrubs, and trees with alternate leaves; flowers irregular; sepals 5; petals 3-5; stamens usually 8; ovary 2-celled; ovules solitary; endosperm present or 0. *Polygala*, *Xanthophyllum*. (Pf. 3⁴: 323.)

Family 102. **Tremandraceae.** Small shrubs with alternate, opposite, or whorled leaves; flowers regular; sepals and petals 3, 4, or 5 each; stamens twice as many; ovary 2-celled; ovules mostly solitary; endosperm fleshy. *Tremandra*, *Tetratheca*. (Pf. 3⁴: 320.)

Family 103. **Dichapetalaceae.** Trees and shrubs with alternate simple leaves; pistil 2-3-celled; endosperm 0. *Dichapetalum*, *Tapura*. (Pf. 3⁴: 345.)

Family 104. **Euphorbiaceae.** Spurges. Herbs, shrubs, and trees, mostly with a milky juice and alternate or opposite leaves; flowers diclinous, with a perianth of 1 or 2 whorls, or wanting; stamens 2-celled, free or united; pistil usually 3-celled; ovules mostly solitary; endosperm copious. *Euphorbia*, *Pedilanthus*, *Phyllanthus*, *Croton*, *Mallotus*, *Acalypha*, *Ricinus*, *Jatropha*, *Manihot*, *Stillingia*. (Species 4319.) (Pf. 3⁵: 1.)

Family 105. **Callitrichaceae**. Floating herbs with opposite sessile leaves; flowers diclinous, sessile in the leaf-axils; perianth none; stamens 1 or 2; ovary 2-celled; endosperm fleshy. *Callitriche*. (Pf. 3⁵:120.)

Order GUTTIFERALES. Pistil mostly of 2 or more carpels, 2-several-celled, with axile placentae; stamens usually indefinite; endosperm usually wanting. (Species about 3138.)

Family 106. **Theaceae**. Teas. Trees and shrubs usually with alternate leaves; inflorescence various; petals imbricated; seeds few; endosperm scanty or 0. *Thea*, *Stuartia*. (Pf. 3⁶:175.)

Family 107. **Cistaceae**. Herbs and shrubs with opposite (or alternate) leaves; sepals 3-5; petals 5; stamens many; pistil 3-5-carpellary, with as many parietal placentae; seeds usually many, endospermous. *Cistus*, *Helianthemum*, *Hudsonia*. (Pf. 3⁶:299.)

Family 108. **Guttiferaceae**. Trees, shrubs, and rarely herbs, with opposite or whorled, glandular-dotted leaves; inflorescence often trichotomous, with flowers mostly diclinous; petals 2-6, or more, imbricated or contorted; stamens many; carpels mostly 3-5; endosperm 0. *Hypericum*, *Mammea*, *Clusia*, *Garcinia*. (Pf. 3⁶:194.)

Family 109. **Eucryphiaceae**. Evergreen trees of the southern hemisphere, with opposite leaves; flowers large, tetramerous; stamens many; pistil many-celled; seeds endospermous. *Eucryphia*. (Pf. 3⁶:129.)

Family 110. **Ochnaceae**. Tropical shrubs and trees with alternate, coriaceous, simple leaves; pistil lobed, 1-10-celled; endosperm fleshy or 0. *Ochna*. (Pf. 3⁶:131.)

Family 111. **Dipterocarpaceae**. Tropical, resiniferous trees and shrubs with alternate leaves; inflorescence paniced; flowers regular, perfect; petals contorted; fruiting calyx enlarged, and wing-like; carpels few (3-1); seeds 2 in each cell; endosperm 0. *Dipterocarpus*. (Pf. 3⁶:243.)

Family 112. **Caryocaraceae**. Tropical trees and shrubs, with alternate trifoliate leaves, large showy flowers, and many

long stamens; seeds solitary; endosperm scanty or 0. *Caryocar*. (Pf. 3⁶:153.)

Family 113. **Quinaceae**. South American trees and shrubs, with opposite or whorled simple leaves; sepals 4-5; petals 4-5; stamens 15-30. *Quina*. (Pf. 3⁶:165.)

Family 114. **Marcgraviaceae**. Tropical trees and shrubs, with alternate, simple leaves; sepals 2-6; petals as many; stamens as many or more; ovary 3-5-celled; seeds many; endosperm 0. *Marcgravia*. (Pf. 3⁶:157.)

Family 115. **Flacourtiaceae**. Mostly tropical trees and shrubs with alternate leaves; sepals 2-15; petals 10-0; stamens indefinite; carpels 2-10; seeds endospermous. *Pangium*, *Flacourtia*, *Samyda*. (Pf. 3^{6a}:1.)

Family 116. **Bixaceae**. Tropical shrubs with alternate leaves; sepals 3-7; petals large; stamens indefinite; pistil bicarpellary; seeds endospermous. *Bixa*. (Pf. 3⁶:307.)

Family 117. **Cochlospermaceae**. Tropical trees and shrubs with alternate lobed or compound leaves; petals large; stamens indefinite; pistil 3-5-carpellary; endosperm copious. *Cochlospermum*. (Pf. 3⁶:312, and Nachträge zu Teil II-IV, 251.)

Family 118. **Violaceae**. Violets. Herbs and shrubs with alternate (or opposite) leaves; sepals and petals 5, irregular; stamens 5; pistil 3-carpellary with 3 parietal placentae; endosperm copious. *Rinorea*, *Hybanthus*, *Viola*. (Pf. 3⁶:322.)

Family 119. **Malesherbiaceae**. South American branching herbs or undershrubs, with perfect, regular, pentamerous flowers; endosperm fleshy. *Malesherbia*. (Pf. 3^{6a}:65.)

Family 120. **Turneraceae**. Tropical herbs and shrubs with alternate leaves; flowers perfect; sepals and petals dissimilar; stamens definite; ovary tricarpeal; endosperm copious. *Turnera*. (Pf. 3^{6a}:57.)

Family 121. **Passifloraceae**. Passion flowers. Climbing herbs and shrubs (a few trees) with alternate leaves; flowers perfect, regular; sepals and petals similar, distinct; stamens definite; ovary free; endosperm fleshy. *Adenia*, *Passiflora*. (Pf. 3^{6a}:69.)

Family 122. **Achariaceae**. South African herbs and undershrubs, related to the *Passifloraceae*; but with the petals united. *Acharia*. (Pf. 3^{6a}:92.)

Family 123. **Caricaceae**. Papaws. Succulent-stemmed tropical trees, mostly with palmate leaves and milky juice; flowers pentamerous; fruit a many seeded berry; endosperm fleshy. *Carica*. (Pf. 3^{6a}:94.)

Family 124. **Stachyuraceae**. Asiatic shrubs and trees with alternate leaves; sepals 4; petals 4; stamens 8; endosperm fleshy. *Stachyurus*. (Pf. 3⁶:192.)

Family 125. **Koeberliniaceae**. Leafless, thorny Texan and Mexican shrubs, with tetramerous flowers; pistil bicarpellary; seeds many; endosperm scanty. *Koeberlinia*. (Pf. 3⁶:319.)

Order RHOEADALES. Pistil of 2 or more united carpels, mostly 1-celled, with parietal placentae; stamens indefinite or definite; endosperm none or copious. (Species about 2856.)

Family 126. **Papaveraceae**. Poppies. Mostly milky-juiced plants, with alternate leaves, and regular or irregular flowers; sepals 2-3; petals 4 or more (or 0); stamens indefinite; pistil many-carpellary; seeds usually many; endosperm fleshy. *Eschscholtzia*, *Sanguinaria*, *Argemone*, *Papaver*, *Bicuculla*, *Fumaria*. (Pf. 3²:130.)

Family 127. **Tovariaceae**. Annual herbs of the tropics, with alternate leaves; 8-merous flowers, and many seeds, with scanty endosperm. *Tovaria*. (Pf. 3²:207.)

Family 128. **Nymphaeaceae**. Water-lilies. Aquatic herbs with floating leaves, and regular flowers; petals present, in 1-many whorls (really acyclic); pistils closely united; seeds many, endospermous. *Victoria*, *Castalia*, *Nymphaea*. (Pf. 3²:1.)

Family 129. **Moringaceae**. Trees of the tropics, with decompound leaves and pentamerous, zygomorphic flowers, and producing bean-like tricarpeal pods; endosperm 0. *Moringa*. (Pf. 3²:242.)

Family 130. **Resedaceae**. Mignonettes. Herbs and shrubs with scattered leaves and zygomorphic flowers; sepals 4-8

(or 2 or 0); stamens 3–40; pistil 2–6-carpellary; seeds many; endosperm 0. *Reseda*. (Pf. 3²: 237.)

Family 131. **Capparidaceae**. Capers. Herbs, shrubs, and trees with alternate or opposite leaves, and regular or irregular flowers; sepals 4; petals 4 (or 0); stamens 4 (or many); pistil 2–6-carpellary, endosperm 0. *Cleome*, *Capparis*. (Pf. 3²: 209.)

Family 132. **Brassicaceae**. Mustards. Herbs, rarely shrubs, with alternate (or opposite) leaves, and regular flowers; sepals 4; petals 4; stamens 6 or 4; pistil 2-carpellary; endosperm 0. *Sinapis*, *Brassica*, *Raphanus*, *Bursa*, *Alyssum*. (Pf. 3²: 145.)

Order CARYOPHYLLALES. Pistil usually of 3 or more united carpels, mostly 1-celled, with a free-central placenta, and many ovules (sometimes reduced to a one-celled, one-ovuled ovary); stamens as many or twice as many as the petals; flowers regular; seeds mostly endospermous, usually with a curved embryo. (Species about 4330.)

The general arrangement of the families of the order *Caryophyllales* may be understood by placing the *Caryophyllaceae* centrally at the base; from this, one line runs off to the diploclamydeous, hermaphrodite *Frankeniaceae* and *Tamariaceae* to the achlamydeous, diclinous *Salicaceae*, while on the other hand another line passes from the diploclamydeous, many-ovuled *Caryophyllaceae* to the apetalous, 1-ovuled *Amaranthaceae*, *Chenopodiaceae* and *Polygonaceae*.

Family 133. **Caryophyllaceae**. Pinks. Herbs (and shrubs) with opposite leaves; petals 3–5, stalked or not; ovules many on a central placenta; seeds endospermous. *Silene*, *Lychnis*, *Dianthus*, *Alsine*, *Paronychia*, *Illecebrum*. (Pf. 3^{1b}: 61.)

Family 134. **Elatinaceae**. Small marsh herbs or undershrubs, with small, opposite or whorled leaves; inflorescence axillary; petals imbricated; stamens 4–10; endosperm 0. *Elatine*. (Pf. 3⁶: 277.)

Family 135. **Portulacaceae**. Purslanes. Herbs, or somewhat woody plants, usually somewhat succulent, with alternate or opposite leaves; sepals usually 2; petals 4–5; seeds many, endospermous. *Claytonia*, *Portulaca*. (Pf. 3^{1b}: 51.)

Family 136. **Aizoaceae**. Herbaceous or shrubby plants with mostly opposite or verticillate, often fleshy leaves; calyx tetramerous or pentamerous; corolla often wanting; ovary mostly 2-5-celled with few to many ovules in each cell; seeds endospermous. *Mollugo*, *Sesuvium*, *Mesembrianthemum*. (Pf. 3^{1b}: 33.)

Family 137. **Frankeniaceae**. Herbs and undershrubs with opposite leaves, and perfect flowers; petals 4-5, long-stalked; ovules many, on 2-4 parietal placentae; seeds endospermous. *Frankenia*. (Pf. 3⁶: 283.)

Family 138. **Tamaricaceae**. Tamarixes. Shrubs and herbs with minute, alternate, deciduous leaves and mostly racemose, perfect flowers; petals 5; ovules many, on 2-5 parietal placentae; seeds hairy-tufted; endosperm 0. *Tamarix*. (Pf. 3⁶: 289.)

Family 139. **Salicaceae**. Willows. Shrubs and trees with large alternate leaves and racemose flowers; perianth 0; ovules many, on 2-4 parietal placentae; seeds hairy-tufted; endosperm 0. Here regarded as reduced, dioecious, apetalous, *Tamaricaceae*. *Salix*, *Populus*. (Pf. 3¹: 29.)

Family 140. **Podostemonaceae**. Riverweeds. Small aquatic, sometimes thallose, plants; flowers perfect or diclinous; perianth 0; pistil 1-3-celled; ovules many, centrally attached; endosperm 0. *Podostemon*. (Pf. 3^{2a}: 1.)

Family 141. **Hydrostachydaceae**. Large tuber-forming Madagascar plants, with naked, dioecious flowers, single stamens, and numerous ovules on 2 parietal placentae; endosperm 0. *Hydrostachys*. (Pf. 3^{2a}: 22.)

Family 142. **Phytolaccaceae**. Pokeweeds. Herbs, shrubs, and trees with usually alternate leaves; petals 0 (or 4-5); carpels several, distinct or nearly so, 1-ovuled; seeds endospermous. *Phytolacca*. (Pf. 3^{1b}: 1.)

Family 143. **Basellaceae**. Herbaceous climbing plants, with mostly alternate leaves; calyx dimerous; corolla pentamerous; stamens 5; ovary tricarpeal, 1-celled, with one ovule; endosperm scanty. *Basella*, *Boussingaultia*. (Pf. 3^{1a}: 124.)

Family 144. **Amaranthaceae.** Amaranths. Herbs, shrubs (and trees) with opposite or alternate leaves, and regular, mostly perfect flowers; perianth of scarious sepals; petals 0; ovules 1 or more, basal, campylotropous; endosperm copious. *Celosia*, *Amaranthus*, *Froelichia*. (Pf. 3^{1a}: 91.)

Family 145. **Chenopodiaceae.** The Goosefoots. Herbs, shrubs (and trees) with mostly alternate leaves, and regular, perfect or imperfect flowers; perianth of herbaceous sepals; petals 0; ovule 1, basal, campylotropous; endosperm fleshy. *Beta*, *Chenopodium*, *Spinacia*, *Atriplex*, *Sarcobatus*, *Salsola*. (Pf. 3^{1a}: 36.)

Family 146. **Polygonaceae.** Buckwheats. Herbs, shrubs, and trees with mostly alternate leaves and regular, perfect flowers; perianth often petaloid; petals 0; pistil tricarpeillary, 1-celled; ovule 1, erect, orthotropous; endosperm copious. *Eriogonum*, *Rumex*, *Rheum*, *Polygonum*, *Fagopyrum*, *Coccoloba*. (Pf. 3^{1a}: 1.)

Family 147. **Nyctaginaceae.** Four o'clocks. Herbs and rarely shrubs and trees, with opposite or alternate leaves; flowers mostly perfect; petals 0; sepals often petaloid; pistil seemingly monocarpellary; ovule 1, erect; endosperm copious to scanty. *Mirabilis*, *Bougainvillea*, *Allionia*. (Pf. 3^{1b}: 14.)

Family 148. **Cynocrambaceae.** Annual, succulent herbs, with petioled leaves, opposite below, alternate above; flowers monoecious, apetalous, small, axillary; pistil monocarpellary; endosperm fleshy. *Cynocrambe*. (Pf. 3^{1a}: 121.)

Family 149. **Batidaceae.** Maritime shrubs with opposite fleshy leaves and small, dioecious flowers; petals 0; ovary 4-celled; ovule solitary, erect; endosperm 0. Very doubtfully placed here. *Batis*. (Pf. 3^{1a}: 118.)

Super-Order STROBILOIDEAE-SYMPETALAE-POLYCARPELLATAE.
Carpels typically many, united; petals united. Flowers actinomorphic.

Order EBENALES. Flowers regular, perfect, or diclinous; stamens mostly isomereous with, and opposite to, the corolla-lobes, or in several series; ovary 2-many-celled; seeds mostly

solitary or few, usually large, centrally attached. (Species about 1136.)

Family 150. **Sapotaceae**. Sapodillas. Tropical trees and shrubs with a milky juice, and mostly alternate leaves; flowers mostly perfect; sepals and petals 4-8 each; stamens in 2-3 whorls, attached to the corolla; ovary superior, several-celled; endosperm from fleshy to 0. *Achras*, *Sideroxylon*, *Chrysophyllum*, *Mimusops*. (Pf. 4¹:126.)

Family 151. **Ebenaceae**. Ebonies. Tropical and subtropical trees and shrubs, with very hard wood, and mostly alternate leaves; flowers mostly dioecious; sepals and petals 3-7 each; stamens usually many and free from the corolla; ovary 3-many-celled, superior; endosperm copious. *Diospyros*, *Maba*. (Pf. 4¹:153.)

Family 152. **Symplocaceae**. Tropical and subtropical trees and shrubs, with mostly perfect flowers; sepals usually 5; petals usually 5; stamens many, attached to the base of the corolla; ovary 2-5-celled, inferior; seeds few, endospermous. *Symplocos*. (Pf. 4¹:165.)

Family 153. **Styracaceae**. Styraxes. Trees and shrubs of warm climates with alternate leaves; flowers mostly perfect, sepals and petals 5 each; stamens usually many, attached to the base of the corolla; ovary 3-5-celled, usually inferior; seeds few, endospermous. *Halesia*, *Styrax*. (Pf. 4¹:172.)

Family 154. **Fouquieriaceae**. Mexican shrubs with small leaves (becoming thorn-like), and paniced tubular flowers; sepals 5; petals 5, united into a tube; stamens 10-15, free; ovary tricarpellary; placenta central; seeds few; endosperm scanty. This small family is given place here with some confidence that it is much more closely related to these families than to those of the *Caryophyllales* and *Polemoniales*, with which it has been associated. *Fouquieria*. (Pf. 3⁶:298.)

Order ERICALES. Flowers regular, perfect, pentamerous or tetramerous; stamens alternate with the corolla-lobes, and as many or twice as many; cells of the mostly superior ovary (or placentae) 2 to many; seeds minute. (Species about 1730.)

Family 155. **Clethraceae**. White alders. Shrubs and trees of warm climates, with alternate deciduous leaves and pentamerous flowers; stamens 10; pistil tricarpellary; endosperm fleshy. *Clethra*. (Pf. 4¹:1.)

Family 156. **Ericaceae**. Heaths. Shrubs and small trees with mostly evergreen alternate or opposite leaves; ovary typically superior (sometimes inferior), 2-10-celled; anthers usually dehiscent by an apical pore; endosperm fleshy. *Rhododendron*, *Kalmia*, *Gaultheria*, *Arctostaphylos*, *Gaylussacia*, *Vaccinium*, *Calluna*, *Erica*. (Pf. 4¹:15.)

Family 157. **Epacridaceae**. Shrubs and small trees (mostly Australian) with mostly alternate evergreen leaves; ovary superior, mostly 2-10-celled; fruit capsular or drupaceous; anthers dehiscent by a slit; endosperm fleshy. *Epacris*. (Pf. 4¹:66.)

Family 158. **Diapensiaceae**. Low undershrubs, with alternate evergreen leaves; ovary superior, 3-celled; fruit a capsule; anthers dehiscent by a slit; endosperm fleshy. *Diapensia*, *Shortia*. (Pf. 4¹:80.)

Family 159. **Pirolaceae**. Wintergreens. Low evergreen, or chlorophyllless herbs, with pentamerous or tetramerous (rarely hexamerous) flowers; stamens twice as many as the petals; ovary 4-6-celled; endosperm fleshy. *Pirola*, *Chimaphila*, *Monotropa*. (Pf. 4¹:3.)

Family 160. **Lennoaceae**. Parasitic, leafless herbs; ovary superior, 10-14-carpellary, 20-28-celled; ovules solitary; anthers dehiscent by a slit; endosperm copious. *Lennoa*. (Pf. 4¹:12.)

Order PRIMULALES. Flowers regular, mostly perfect and pentamerous; stamens epipetalous, mostly opposite to the corolla-lobes; ovary pluricarpellary, mostly 1-celled, with a free-central placenta. (Species about 1581.)

Family 161. **Primulaceae**. Primroses. Herbs with alternate or opposite leaves; stamens attached to the upper portion of the corolla tube; pistil 2-6-carpellary, one-celled; ovules many; fruit a capsule dehiscent longitudinally from the apex,

or circumscissilely; endosperm fleshy. *Primula*, *Androsace*, *Lysimachia*, *Cyclamen*, *Dodecatheon*. (Pf. 4¹:98.)

Family 162. **Plantaginaceae**. Plantains. Herbs with clustered radical leaves, or alternate or opposite stem leaves; stamens alternate with the petals; ovary mostly 2-celled; ovules many; placenta axile; fruit a capsule dehiscing circumscissilely; endosperm fleshy. *Plantago*. (Pf. 4^{3b}:363.)

Family 163. **Plumbaginaceae**. Leadworts. Herbs with alternate or clustered leaves; stamens opposite the petals; pistil 5-carpellary, one-celled, with one basal, anatropous ovule; fruit capsular; dehiscence valvate or irregular; endosperm copious. *Plumbago*, *Armeria*. (Pf. 4¹:116.)

Family 164. **Myrsinaceae**. Trees and shrubs with mostly alternate leaves; stamens attached to the lower part of the corolla tube; ovules usually few; fruit a drupe or berry; endosperm fleshy. *Myrsine*, *Ardisia*. (Pf. 4¹:84.)

Family 165. **Theophrastaceae**. Tropical trees and shrubs closely related to the preceding family, and sometimes included in it, but with many ovules. *Theophrasta*, *Jacquinia*. (Pf. 4¹:88.)

Super-Order STROBILOIDEAE-SYMPETALAE-DICARPELLATAE. Carpels typically two, united; petals united. Flowers mostly perfect, from actinomorphic to zygomorphic.

Order GENTIANALES. Corolla actinomorphic (regular), mostly pentamerous; stamens alternate with the corolla-lobes, and usually of the same number and attached to the tube; leaves opposite (rarely alternate). (Species about 4664.)

Family 166. **Oleaceae**. Olives. Shrubs and trees (rarely herbs) with mostly opposite leaves, and tetramerous flowers; corolla-lobes mostly valvate or 0; stamens 2 (or 4); ovary 2-celled; ovules 1-3; endosperm present or 0. *Syringa*, *Olea*, *Jasminum*, *Fraxinus*. (Pf. 4²:1.)

Family 167. **Salvadoraceae**. Mostly tropical shrubs and trees, with opposite undivided leaves, and tetramerous or pentamerous flowers; corolla-lobes imbricated; stamens 4; ovary 2-celled; ovules 2; endosperm 0. *Salvadora*. (Pf. 4²:17.)

Family 168. **Loganiaceae.** Herbs, shrubs, and trees with mostly opposite simple leaves and pentamerous or tetramerous flowers; corolla-lobes imbricated or contorted; stamens mostly 4-5; ovary 2-celled (rarely 4-celled); ovules 1-many; endosperm fleshy. *Gelsemium*, *Logania*, *Spigelia*, *Strychnos*. (Pf. 4²: 19.)

Family 169. **Gentianaceae.** Gentians. Mostly herbs, with usually opposite undivided leaves and pentamerous or tetramerous flowers; corolla-lobes contorted, valvate, or induplicate; stamens 4-5; ovary bicarpellary, usually 1-celled; ovules many; endosperm copious. *Erythraea*, *Gentiana*, *Eustoma*, *Menyanthes*. (Pf. 4²: 50.)

Family 170. **Apocynaceae.** Dogbanes. Milky-juiced trees, shrubs, and herbs, with opposite or whorled, simple leaves and mostly pentamerous (rarely tetramerous) flowers; corolla-lobes contorted or valvate; stamens 5 (or 4), with granular pollen; ovary 2-celled or the carpels separating; ovules many; endosperm fleshy. *Vinca*, *Apocynum*, *Nerium*. (Pf. 4²: 109.)

Family 171. **Asclepiadaceae.** Milkweeds. Milky-juiced herbs and shrubs, with opposite, whorled (or alternate) leaves and pentamerous flowers; corolla-lobes contorted; stamens 5, with agglutinated pollen; ovary of two separated carpels with one discoid stigma; ovules many; seeds usually comose; endosperm fleshy. *Asclepias*, *Enslenia*, *Ceropegia*, *Stapelia*, *Hoya*. (Pf. 4²: 189.)

Order POLEMONIALES. Corolla actinomorphic, becoming somewhat zygomorphic in the later families; stamens alternate with the corolla-lobes, of the same number and attached to the corolla tube; leaves alternate (rarely opposite). (Species about 4112.)

The relationship of this order to the *Primulales*, and through it to the *Caryophyllales*, is so obvious as to make it scarcely necessary to point it out here.

Family 172. **Polemoniaceae.** Phloxes. Herbs (and shrubs) with alternate leaves (rarely opposite below); flowers pentamerous; corolla-lobes 5, contorted; ovary tricarpeal, 3-celled;

ovules 1 or more in each cell; endosperm fleshy. *Cobaea*, *Phlox*, *Gilia*, *Polemonium*. (Pf. 4^{3a}:40.)

Family 173. **Convolvulaceae**. Morning-glories. Herbs (often climbing), shrubs (and trees) with alternate leaves and pentamerous flowers; corolla-limb more or less plicate (rarely imbricated); ovary 2 (3–5)-celled; ovules few; endosperm fleshy. *Evolvulus*, *Quamoclit*, *Ipomoea*, *Convolvulus*, *Cuscuta* (parasitic). (Pf. 4^{3a}:1.)

Family 174. **Hydrophyllaceae**. Herbs with radical or alternate (rarely opposite) leaves and pentamerous flowers; corolla-lobes imbricated (or contorted); ovary 1 or incompletely 2-celled; ovules 2 or more; endosperm fleshy. *Hydrophyllum*, *Phacelia*, *Nama*. (Pf. 4^{3a}:54.)

Family 175. **Borraginaceae**. Forget-me-nots. Herbs, shrubs, and trees with alternate leaves and pentamerous flowers; corolla-lobes imbricated (or contorted); ovary bicarpellary, 4-celled, 4-lobed; ovules solitary in each lobe; endosperm fleshy or 0. *Heliotropium*, *Cynoglossum*, *Oreocarya*, *Borrage*, *Myosotis*, *Mertensia*, *Lithospermum*. (Pf. 4^{3a}:71.)

Family 176. **Nolanaceae**. Herbaceous or suffrutescent prostrate South American plants, with alternate, entire leaves; calyx 5-parted; corolla long funnel-shaped; stamens 5, inserted on the corolla; carpels 5, distinct or united; endosperm fleshy. *Nolana*. (Pf. 4^{3b}:1.)

Family 177. **Solanaceae**. Nightshades. Herbs, shrubs (and trees) with alternate leaves and pentamerous, mostly regular, but sometimes irregular flowers; corolla-limb more or less plicate (rarely imbricated); ovary mostly 2-celled; ovules many; endosperm fleshy. *Lycium*, *Atropa*, *Hyoscyamus*, *Physalis*, *Capsicum*, *Solanum*, *Datura*, *Nicotiana*, *Petunia*. (Pf. 4^{3b}:4.)

Order SCROPHULARIALES. Corolla mostly zygomorphic (irregular or oblique); stamens fewer than the corolla-lobes, usually 4 or 2; ovules numerous; fruit mostly capsular (i. e., dehiscent). (Species about 7081.)

Family 178. **Scrophulariaceae**. Snapdragons. Herbs (or shrubs and small trees) with alternate, opposite, or whorled

leaves; ovary 2-celled with an axile placenta; seeds numerous, with endosperm. *Verbascum*, *Linaria*, *Antirrhinum*, *Maurandia*, *Collinsia*, *Scrophularia*, *Mimulus*, *Veronica*, *Digitalis*, *Gerardia*, *Castilleja*, *Pedicularis*. (Pf. 4^{3b}:39.)

Family 179. **Bignoniaceae**. Catalpas. Trees, shrubs (and herbs) with opposite or whorled leaves; ovary 1 or 2-celled with parietal or axile placentae; seeds numerous, without endosperm. *Bignonia*, *Catalpa*, *Tecoma*. (Pf. 4^{3b}:189.)

Family 180. **Pedaliaceae**. Mostly tropical herbs with generally opposite leaves; ovary 1, 2, or 4-celled with axile placentae; seeds 1-many, with but little endosperm. *Pedaliium*, *Sesamum*. (Pf. 4^{3b}:253.)

Family 181. **Martyniaceae**. Mostly tropical herbs with generally opposite leaves; stamens 2 or 4; ovary 1-celled with projecting parietal placentae; endosperm 0. *Martynia*. (Pf. 4^{3b}:265.)

Family 182. **Orobanchaceae**. Broom-rapes. Leafless parasitic herbs; ovary 1-celled; placentae 4, parietal; ovules minute, numerous; endosperm fleshy. *Orobanche*, *Thalesia*, *Conopholis*. (Pf. 4^{3b}:123.)

Family 183. **Gesneraceae**. Tropical and subtropical herbs, shrubs (and trees) with usually opposite leaves; ovary inferior or superior, 1-celled, with 2 parietal placentae; seeds numerous; endosperm scanty or 0. *Streptocarpus*, *Gesnera*, *Gloxinia*. (Pf. 4^{3b}:133.)

Family 184. **Columelliaceae**. South American trees and shrubs with opposite, evergreen leaves and nearly regular flowers; stamens 2; ovary inferior, 2-celled, with an axile placenta; endosperm fleshy. *Columellia*. (Pf. 4^{3b}:186.)

Family 185. **Lentibulariaceae**. Bladderworts. Aquatic or marsh herbs with basal, entire or dissected leaves and irregular flowers; ovary 1-celled, with a globose basilar placenta; seeds numerous; endosperm 0. *Pinguicula*, *Utricularia*. (Pf. 4^{3b}:108.)

Family 186. **Globulariaceae**. Shrubs and undershrubs or evergreen herbs, with alternate leaves, and a terminal capitate

cluster of small irregular flowers; ovary 1-celled, with a single ovule; endosperm fleshy. *Globularia*. (Pf. 4^{3b}:270.)

Family 187. **Acanthaceae**. Herbs (shrubs and trees) with opposite leaves; ovary 2-celled; placentae axile; fruit a dry pod which splits open vertically; seeds 2-many, without endosperm. *Thunbergia*, *Ruellia*, *Acanthus*, *Justicia*. (Pf. 4^{3b}:274.)

Order LAMIALES. Corolla mostly zygomorphic (irregular or oblique); stamens fewer than the corolla-lobes, usually 4 or 2; ovules mostly 2 in each carpel; fruit indehiscent. (Species about 4119.)

Family 188. **Myoporaceae**. Mostly Australasian shrubs and trees, with usually alternate leaves; flowers axillary; fruit a 1-4-seeded drupe; endosperm scanty. *Myoporum*. (Pf. 4^{3b}:354.)

Family 189. **Phrymaceae**. Erect, perennial herbs, with opposite leaves, and small spicate flowers; calyx and corolla cylindrical, 2-lipped; stamens 4; ovary 1-celled, 1-ovuled; stigma bifid; endosperm 0. *Phryma*. (Pf. 4^{3b}:361.)

Family 190. **Verbenaceae**. Verbenas. Herbs, shrubs, and trees, with usually opposite leaves; ovary of 2 carpels, but 2-8-celled, with 1 ovule in each cell; stigma usually undivided; endosperm scanty or 0. *Verbena*, *Lantana*, *Lippia*, *Tectona*, *Vitex*. (Pf. 4^{3a}:132.)

Family 191. **Lamiaceae**. Mints. Mostly aromatic herbs, shrubs (and trees) with opposite or whorled leaves; ovary 4-celled, 4-lobed with 1 ovule in each cell; stigma usually bifid; endosperm scanty or 0. *Lavendula*, *Nepeta*, *Stachys*, *Salvia*, *Thymus*, *Mentha*, *Coleus*. (Pf. 4^{3a}:183.)

With this order (*Lamiales*), and especially with this family (*Lamiaceae*), we attain the summit of the cone-flowers (*Strobiloideae*). We next return almost to the point of beginning, and there start on a new phyletic line.

Sub-Class OPPOSITIFOLIAE - COTYLOIDEAE. "Cup Flowers." Axis of the flower normally expanded into a disk or cup, bearing on its margin the perianth and stamens (or the latter may be attached to the corolla).

Super-Order COTYLOIDEAE - APOPETALAE. Petals separate. Carpels many to few, separate to united, superior to inferior. This super-order appears to have originated near the beginning of the *Strobiloideae*, and therefore the orders *Ranales* and *Rosales* are to be regarded as closely related. Their relationship to *Alismatales*, also, has already been pointed out.

Order ROSALES. Flowers cyclic, usually perfect, dichlamydeous (rarely apetalous), actinomorphic to zygomorphic (regular to irregular) and mostly pentamerous; carpels usually several to many, separate or more or less united, sometimes united with the axis-cup (rarely reduced to 1); styles usually distinct. (Species about 14261.)

Family 192. **Rosaceae**. Roses. Herbs, shrubs, and trees with mostly alternate leaves; stamens usually indefinite, on the cup-margin; carpels several to many (rarely 1), free (but they may be enclosed in the deep cup); ovules usually 2, anatropous; endosperm 0. *Potentilla*, *Fragaria*, *Spiraea*, *Rosa*. (Species about 2700.) (Pf. 3³:1.)

Family 193. **Malaceae**. Apples. Shrubs and trees with alternate leaves; stamens usually many on the cup-margin; carpels few, more or less united, and adnate to the axis-cup, so as to be "inferior"; endosperm 0. *Sorbus*, *Pirus*, *Malus*, *Crataegus*. (Pf. 3³:1, 18.)

Family 194. **Prunaceae**. Plums. Shrubs and trees with alternate leaves; stamens many, on the cup-margin; carpel one, in the bottom of the deep cup, becoming a drupe; endosperm 0. *Prunus*, *Amygdalus*. (Species 150.) (Pf. 3³:1, 50.)

Family 195. **Crossosomataceae**. Southwest North American shrubs, with small leaves and a bitter bark; sepals and petals 5 each; stamens 20 or more; carpels 3-5; seeds many, reniform; endosperm scanty. *Crossosoma*. (Pf. Nachträge zu Teil II-IV, 185.)

Family 196. **Connaraceae**. Tropical trees and shrubs with alternate compound leaves; stamens definite (5-10); pistils mostly 5, free; ovules 2, ascending, orthotropous; endosperm fleshy or 0. *Connarus*, *Cnestis*. (Pf. 3³:61.)

Family 197. **Mimosaceae**. The mimosas. Mostly tropical trees, shrubs, and herbs, with alternate mostly compound leaves; flowers actinomorphic; stamens 10 or more, usually separate; carpel 1; fruit a legume; seeds mostly without endosperm. *Acacia*, *Mimosa*. (Species 1483.) (Pf. 3³: 70, 99.)

Family 198. **Cassiaceae**. The sennas. Mostly tropical trees, shrubs, and herbs, with alternate mostly compound leaves; flowers zygomorphic; stamens 10 or less, usually separate; carpel 1; fruit a legume; seeds with or without endosperm. *Cassia*, *Caesalpinia*, *Gleditsia*, *Gymnocladus*. (Species 1172.) (Pf. 3³: 70, 125.)

Family 199. **Fabaceae**. The beans. Mostly herbs of temperate climates, but with many shrubs and trees; leaves alternate, mostly compound; flowers zygomorphic; stamens 10 or less, usually more or less united; carpel 1; fruit a legume; seeds usually without endosperm. *Lupinus*, *Medicago*, *Trifolium*, *Robinia*, *Astragalus*, *Arachis*, *Vicia*, *Pisum*, *Phaseolus*. (Species 6948.) (Pf. 3³: 70, 184.)

This family constitutes a well-marked side-line in the order *Rosales*, with zygomorphic, entomophilous flowers. It is not obvious what relation, if any, exists between this form of the flower, and the legume structure of the fruiting carpel.

Family 200. **Saxifragaceae**. Saxifrages. Herbs with alternate leaves, regular 4 or 5-merous mostly perfect flowers, with 8 or 10 stamens, and usually 2 more or less united carpels which are superior; seeds many; endosperm copious. *Saxifraga*, *Heuchera*, *Mitella*. (Pf. 3^{2a}: 41.)

Family 201. **Hydrangeaceae**. Hydrangeas. Shrubs and trees with mostly opposite leaves, and regular 4 or 5-merous mostly perfect flowers, with few (8) to many (40) stamens, and 2-5 united carpels, which are more or less overgrown by the axis-cup; seeds many; endosperm copious. *Philadelphus*, *Hydrangea*. (Pf. 3^{2a}: 41.)

Family 202. **Grossulariaceae**. Gooseberries. Shrubs with alternate leaves, regular 4 or 5-merous perfect flowers, usually 5 stamens, and 2 to several united carpels which are wholly

overgrown by the fleshy cup (ovary inferior); seeds few, endosperm copious. *Ribes*. (Pf. 3^{2a}: 41.)

Family 203. **Crassulaceae**. Stonecrops. Mostly fleshy herbs, with opposite or alternate leaves and perfect flowers; stamens definite (4-10 or many); pistils several, free or little united; ovules many; placentae central or axile; endosperm fleshy. *Sedum*, *Cotyledon*, *Crassula*, *Penthorum*. (Pf. 3^{2a}: 23.)

Family 204. **Droseraceae**. Sundews. Gland-bearing marsh herbs with perfect flowers; stamens mostly definite (4-20); pistil syncarpous, 1-3-celled, superior; ovules many, on basal, axile, or parietal placentae; endosperm fleshy. *Drosera*, *Dionaea*. (Pf. 3²: 261.)

Family 205. **Cephalotaceae**. Pitcher-plants. Perennial Australian herbs with a rosette of elliptic, and pipe-shaped radical leaves, and a central, erect, spicate flowering stem; flowers regular, perfect, apetalous; sepals 6; ovules solitary; endosperm copious. *Cephalotus*. (Pf. 3^{2a}: 39.)

Family 206. **Pittosporaceae**. Trees and shrubs of the southern hemisphere, with alternate leaves; sepals, petals, and stamens 5 each; ovary 2-carpellate; endosperm copious. *Pittosporum*, *Marianthus*. (Pf. 3^{2a}: 106.)

Family 207. **Brunelliaceae**. South American trees, with opposite or whorled leaves and diclinous flowers; sepals and petals 4-5 or 7 each; stamens twice as many; carpels usually 4-5, free; endosperm fleshy. *Brunellia*. (Pf. Nachträge zu Teil II-IV, 182.)

Family 208. **Cunoniaceae**. Shrubs and trees, mostly of the southern hemisphere, with opposite or whorled leaves and small, perfect flowers; sepals and petals 4-6 each; stamens twice as many; carpels 2-5, united; endosperm fleshy. *Belangeria*, *Cunonia*. (Pf. 3^{2a}: 94.)

Family 209. **Myrothamnaceae**. Small, rigid, balsamic South African and Madagascar shrubs, with opposite leaves, and dioecious, achlamydeous flowers; ovary tricarpellary; seeds many, with fleshy endosperm. *Myrothamnus*. (Pf. 3^{2a}: 103.)

Family 210. **Bruniaceae**. Heath-like shrubs of the southern hemisphere, with small leaves and small, perfect, regular, pentamerous flowers; stamens definite; pistil 2–3-celled, inferior or superior; ovules 1 to many, pendulous; endosperm copious. *Brunia*. (Pf. 3^{2a}:131.)

Family 211. **Hamamelidaceae**. Witch-hazels. Shrubs and trees with mostly alternate leaves and perfect or imperfect, mostly pentamerous flowers; stamens few or many; pistil bicarpellary, its ovary inferior; ovules solitary or many; endosperm thin. *Liquidambar*, *Altingia*, *Hamamelis*. (Pf. 3^{2a}:115.)

Family 212. **Casuarinaceae**. Beefwood trees. Shrubs and trees with striate stems bearing whorls of reduced scale-like leaves; flowers diclinous; petals 0; pistil bicarpellary, 1-celled; ovules 2, lateral, half anatropous; endosperm 0. *Casuarina*. (Pf. 3¹:16.) This family, which has puzzled botanists from the first, is doubtfully placed here, on the theory that these plants are leafless relatives of the *Hamamelidaceae*.

Family 213. **Eucommiaceae**. Chinese trees, with alternate leaves, and achlamydeous diclinous flowers; stamens 6–10; pistil bicarpellary, 1-celled, 2-seeded; endosperm present. *Eucommia*. (Pf. Nachträge zu Teil II–IV, 159.)

Family 214. **Platanaceae**. Plane-trees. Trees with alternate leaves, and monoecious flowers in globular heads; perianth 3–8-merous; stamens 3–8; pistils 3–8, each 1-celled, 1-ovuled; endosperm scanty. *Platanus*. (Pf. 3^{2a}:137.)

Order MYRTALES. Flowers usually actinomorphic (regular) or nearly so, usually perfect; pistil of united carpels, usually inferior; placentae axile or apical (rarely basal); style 1 (rarely several); leaves simple, usually entire. (Species about 7323.)

Here again we shall soon reach the end of a phyletic sideline, consisting principally of the order *Myrtales*, with the *Loasales* and *Cactales* as the ultimate branches.

Family 215. **Lythraceae**. Herbs, shrubs, and trees usually with opposite leaves and 4-angled branches; flowers mostly 4–6-merous; stamens definite (8–12), or indefinite; pistil 2–6-

celled, free; ovules numerous, on axile placentae; endosperm 0. *Lythrum*, *Cuphea*, *Lagerstroemia*. (Pf. 37:1.)

Family 216. **Sonneratiaceae**. Tropical trees with opposite leaves; ovary sunken in the axis-cup, many celled (4-15); stamens many; endosperm 0. *Sonneratia*. (Pf. 37:16.)

Family 217. **Punicaceae**. Pomegranates. Small tropical and sub-tropical trees with opposite leaves and 5-7-merous flowers; stamens many; ovary inferior, 4-15-celled, producing a pulpy, many-seeded fruit; endosperm 0. *Punica*. (Pf. 37:22.)

Family 218. **Lecythidaceae**. Tropical trees, with alternate leaves and usually 4-6-merous flowers; stamens many; ovary inferior, 2-6-celled; endosperm 0. *Barringtonia*, *Napoleona*, *Lecythis*, *Bertholletia*. (Pf. 37:26.)

Family 219. **Melastomataceae**. Mostly tropical herbs, shrubs, and trees with generally opposite or whorled leaves; stamens usually double the number of petals; pistil 2-many-celled, inferior; ovules minute, numerous, on axile or parietal placentae; endosperm 0. *Melastoma*, *Osbeckia*, *Rhexia*, *Tamonea*. (Pf. 37:130.)

Family 220. **Myrtaceae**. Myrtles. Trees and shrubs with opposite or alternate leaves, and perfect, regular flowers; stamens many; pistil 2-many-celled, inferior; ovules 2 to many; placentae basal or axile; endosperm 0. *Myrtus*, *Pimenta*, *Eugenia*, *Jambosa*, *Eucalyptus*, *Malaleuca*. (Species 2556.) (Pf. 37:57.)

Family 221. **Combretaceae**. Trees and shrubs often climbing, with opposite or alternate leaves; stamens usually definite (4-10); pistil 1-celled, inferior; ovules 2-6 or solitary, pendulous; endosperm 0. *Terminalia*, *Combretum*, *Laguncularia*. (Pf. 37:106.)

Family 222. **Rhizophoraceae**. Mangroves. Mostly tropical trees and shrubs with opposite leaves and regular, 4-8-merous flowers; stamens 2-4 times the number of petals; pistil 2-6-celled, usually inferior; ovules 2, pendulous; endosperm fleshy. *Rhizophora*, *Carallia*. (Pf. 37:42.)

Family 223. **Oenotheraceae**. Evening primroses. Herbs (shrubs and trees) with opposite or alternate leaves, and perfect, 2-3-4-merous, regular flowers; stamens 1-8, rarely more; pistil usually 4-celled, inferior; ovules 1 to many on axile placentae; endosperm scanty or 0. *Epilobium*, *Anogra*, *Oenothera*, *Meriolix*, *Gaura*, *Fuchsia*, *Circaea*. (Pf. 3⁷:199.)

Family 224. **Halorrhagidaceae**. Aquatic or terrestrial herbs with opposite or alternate leaves and perfect or imperfect, sometimes apetalous flowers; pistil 1-4-celled, inferior; ovules solitary, pendulous; endosperm present. *Halorrhagis*, *Myriophyllum*. (Pf. 3⁷:226.)

Family 225. **Hippuridaceae**. Aquatic perennial erect herbs, with whorled leaves, and small, reduced, axillary apetalous flowers; ovary 1-celled, 1-ovuled; endosperm scanty. *Hippuris*. (Pf. 3⁷:237.)

Family 226. **Cynomoriaceae**. Parasitic rhizomatous fleshy plants with spicate, small, apetalous, diclinous flowers, each with a single ovule; endosperm fleshy. *Cynomorium*. (Pf. 3¹:250.)

Family 227. **Aristolochiaceae**. Dutchman's-pipes. Herbaceous or shrubby plants, with alternate leaves and large, apetalous, perfect, irregular flowers; stamens 6, rarely more; pistil 4 or 6-celled, inferior; ovules numerous, on axile (or protruding parietal) placentae; endosperm copious. *Asarum*, *Aristolochia*. (Pf. 3¹:264.)

Family 228. **Rafflesiaceae**. Fleshy, parasitic herbs, of warm climates, leafless, or nearly so, with mostly imperfect flowers; petals 0, or rarely 4; stamens 8 to many; pistil 1-celled or imperfectly many-celled, inferior; ovules minute, very numerous, on parietal or pendulous, folded placentae; endosperm present. *Rafflesia*, *Cytinus*. (Pf. 3¹:274.)

Family 229. **Hydnoraceae**. Parasitic, succulent, tropical herbs with perfect, 3-4-merous flowers; perianth single, valvate; stamens 3-4, but anthers many; seeds very numerous; endosperm copious. *Hydnora*. (Pf. 3¹:282.)

Order **LOSALES**. Flowers usually actinomorphic, perfect or diclinous; pistil mostly tricarpeal, 1-celled, its ovary usually inferior; placentae parietal and with many ovules; styles free or connate; leaves ample, entire, lobed or dissected. (Species about 1392.)

Family 230. **Loasaceae**. Star-flowers. Herbs (rarely climbing) with opposite or alternate leaves; flowers perfect; sepals and petals dissimilar, mostly 5 each; stamens indefinite, 5-10 or more; ovary 3-7-carpellary, 1-celled; endosperm mostly 0. *Mentzelia*, *Loasa*. (Pf. 3^{6a}:100.)

Family 231. **Cucurbitaceae**. Melons. Mostly climbing or prostrate herbs and undershrubs, with alternate leaves; flowers mostly diclinous and pentamerous; stamens definite (usually 3); ovary mostly tricarpeal; endosperm 0. *Melothria*, *Momordica*, *Luffa*, *Citrullus*, *Cucumis*, *Lagenaria*, *Cucurbita*. (Pf. 4⁵:1.)

Family 232. **Begoniaceae**. Begonias. Mostly erect herbs with alternate leaves; flowers diclinous, more or less zygomorphic; stamens indefinite and numerous, ovary tricarpeal, 3-celled, usually 3-angular; endosperm little or 0. *Begonia*. (Pf. 3^{6a}:121.)

Family 233. **Datisceae**. Herbs or large trees, with alternate leaves; flowers small, and diclinous; stamens 4 to many; ovary 3-8-carpellary; placentae on the walls; seeds small, and many; endosperm scanty. *Datisca*. (Pf. 3^{6a}:150.)

Family 234. **Ancistrocladaceae**. Climbing plants of tropical Asia, with alternate leaves, and small, regular, perfect flowers; petals 5; stamens 5-10; ovary 1-celled, many-seeded; endosperm present. *Ancistrocladus*. (Pf. 3⁶:274.)

Order **CACTALES**. Flowers actinomorphic or very slightly zygomorphic, perfect; stamens many; pistil 4-8-carpous, inferior, 1-celled, with 4-8 parietal placentae; style single, with 2 to many stigmas; endosperm scanty or 0; embryo curved. Fleshy-stemmed plants with leaves mostly small or wanting. (Species about 1168.)

Family 235. **Cactaceae**. Cactuses. Mostly natives of the warmer portions of America; from small herbs to tree-like

dimensions. *Peireskia*, *Opuntia*, *Cereus*, *Carnegiea*, *Echinocactus*, *Melocactus*, *Cactus*, *Rhipsalis*. (Pf. 3^{6a}:156.)

Order CELASTRALES. Receptacle often developing a glandular, annular or turgid disk, which is sometimes adnate to the pistil, in which case the pistil is more or less inferior; pistil 1 to many-celled (rarely apocarpous); ovules 1–3, pendulous or erect; endosperm present or 0. Flowers actinomorphic and mostly perfect. (Species about 2741.)

Family 236. **Rhamnaceae**. Buckthorns. Trees and shrubs often climbing, with alternate or opposite, simple leaves; petals present; disk more or less adnate to the 2–4-celled pistil; ovules 1 or 2, erect; endosperm fleshy. *Zizyphus*, *Rhamnus*, *Ceanothus*, *Phyllica*, *Colletia*. (Pf. 3⁵:393.)

Family 237. **Vitaceae**. Grapes. Climbing shrubs (and trees) with alternate, simple or compound leaves; petals coherent, valvate; pistil superior, 2-celled, 2-ovuled (or 3–6-celled, 1-ovuled); endosperm often ruminant. *Vitis*, *Parthenocissus*, *Cissus*. (Pf. 3⁵:427.)

Family 238. **Celastraceae**. Bittersweets. Shrubs (often climbing) and trees, with usually alternate, simple leaves; petals present, imbricated; disk more or less adnate to the 2–5-celled pistil; ovules usually 2, erect or pendulous; endosperm fleshy. *Euonymus*, *Celastrus*, *Cassine*. (Pf. 3⁵:189.)

Family 239. **Buxaceae**. Boxes. Evergreen shrubs and trees, with alternate or opposite leaves, and usually monoecious, small, apetalous flowers; stamens 4; pistil tricarpeal, superior; endosperm fleshy. *Pachysandra*, *Buxus*. (Pf. 3⁵:130.)

Family 240. **Aquifoliaceae**. Hollies. Trees and shrubs, with alternate or opposite, simple leaves and small, perfect flowers; pistil superior, 3 to many-celled; ovule 1, pendulous; endosperm fleshy. *Ilex*, *Nemopanthes*. (Pf. 3⁵:183.)

Family 241. **Cyrillaceae**. South American evergreen shrubs or small trees, with alternate leaves; sepals 5; petals 5; stamens 5–10; carpels 2–5, united, superior; endosperm fleshy. *Cyrilla*. (Pf. 3⁵:179.)

Family 242. **Pentaphylacaceae**. Chinese trees, with alternate, leathery leaves and small, perfect flowers; sepals 5; petals 5; stamens 5; pistil superior, of 5 carpels, each 2-ovuled; endosperm scanty. *Pentaphylax*. (Pf. Nachträge zu Teil II-IV, 214.)

Family 243. **Corynocarpaceae**. New Zealand trees, with alternate, fleshy, leathery leaves; sepals 5; petals 5; stamens 5; pistil superior, of 2 carpels; endosperm 0. *Corynocarpus*. (Pf. Nachträge zu Teil II-IV, 215.)

Family 244. **Hippocrateaceae**. Tropical trailing and climbing woody plants with opposite leaves; sepals 5; petals 5; stamens 3 or 2 or 5; pistil of 3 carpels more or less adnate to the disk; endosperm 0. *Hippocratea*, *Salacia*. (Pf. 3⁵: 222.)

Family 245. **Stackhousiaceae**. Australian herbs and shrubs with simple alternate leaves and perfect flowers; petals 5; stamens 5; ovary 2-5-celled; ovule 1 in each cell, erect; endosperm fleshy. *Stackhousia*. (Pf. 3⁵: 231.)

Family 246. **Staphyleaceae**. Bladder-nuts. Erect shrubs and trees, with opposite, compound leaves and pentamerous perfect flowers; sepals 5; petals 5; stamens 5; pistil of 2-3 superior carpels; seeds few to many; endosperm fleshy or 0. *Staphylea*, *Turpinia*. (Pf. 3⁵: 258.)

Family 247. **Geissolomataceae**. South African evergreen shrubs, with opposite sessile leaves; sepals 4; petals none; stamens 8; pistil superior, of 4 carpels, each 2-ovuled; endosperm fleshy. *Geissoloma*. (Pf. 3^{6a}: 205.)

Family 248. **Penaeaceae**. South African evergreen heath-like shrubs, with small, opposite leaves and regular, perfect flowers; petals 0; pistil superior, 4-celled; ovules 2-4, erect; endosperm 0. *Penaea*. (Pf. 3^{6a}: 208.)

Family 249. **Oliniaceae**. African shrubs and trees, with thick, leathery, opposite leaves, and small, regular, perfect flowers; sepals 4-5, large; petals 4-5, very small; stamens 4-5; pistil inferior, of 3-5 carpels; endosperm 0. *Olinia*. (Pf. 3^{6a}: 213.)

Family 250. **Thymelaeaceae**. Shrubs, small trees (and herbs), with alternate or opposite, usually coriaceous, simple

leaves and small petalous or apetalous, mostly perfect flowers; pistil superior, 1-5-carpellary, 1-celled; ovule 1, pendulous; endosperm fleshy, sparse, or 0. *Gnidia*, *Thymelaea*, *Daphne*, *Dirca*. (Pf. 3^{6a}:215.)

Family 251. **Hernandiaceae**. Tropical trees and shrubs, with alternate leaves; flowers perfect or monoecious, regular; sepals 4-10; petals none; stamens 3; pistil 1-celled, inferior; ovule 1, pendulous; endosperm 0. *Hernandia*. (Pf. 3²:126.)

Family 252. **Elaeagnaceae**. Oleasters. White or brown-scurfy trees and shrubs, with alternate or opposite, simple leaves and perfect or diclinous flowers; petals 0; pistil 1-celled; ovule 1, ascending; endosperm 0 or scanty. *Elaeagnus*, *Lepargyrea*. (Pf. 3^{6a}:246.)

Family 253. **Myzodendraceae**. South American parasitic shrubs, with alternate, rather small leaves; flowers dioecious, apetalous; stamens 2-3; pistil 1-celled, inferior; endosperm fleshy. *Myzodendron*. (Pf. 3¹:198.)

Family 254. **Santalaceae**. Sandalwoods. Parasitic herbs, shrubs, and trees, with alternate or opposite, simple leaves and small, perfect, or diclinous flowers; epigynous; petals 0; pistil inferior, 1-5-carpellary, 1-celled; ovules 2-5, pendulous; endosperm present. *Santalum*, *Comandra*, *Thesium*. (Pf. 3¹:202.)

Family 255. **Opiliaceae**. Shrubs of tropical climates, with alternate leaves, and perfect flowers; sepals, petals and stamens 4-5 each; pistil superior, 1-celled, 1-ovuled; endosperm fleshy. *Opilia*. (Pf. Nachträge zu Teil II-IV, 142.)

Family 256. **Grubbiaceae**. South African shrubs with opposite leaves, and epigynous, apetalous flowers; ovary 2-celled; ovules 2; endosperm fleshy. *Grubbia*. (Pf. 3¹:282.)

Family 257. **Olacaceae**. Trees and shrubs, often twining, mostly tropical, with usually alternate, simple leaves and mostly perfect, apetalous flowers; pistil superior or inferior, 1-3-celled; ovules 2-3, pendulous; endosperm fleshy. *Olax*. (Pf. 3¹:231.)

Family 258. **Loranthaceae**. Mistletoes. Parasitic evergreen shrubs with opposite (or alternate) leaves, often re-

duced to bracts; flowers perfect or diclinous; petals 0; pistil 1-celled, inferior; ovule 1, erect; endosperm fleshy. *Loranthus*, *Viscum*, *Phoradendron*, *Razoumowskia*. (Pf. 3¹:156.)

Family 259. **Balanophoraceae**. Parasitic, leafless herbs, all tropical, with much reduced, apetalous, monoecious or dioecious flowers; pistil 1-celled, inferior; ovule 1, pendulous; endosperm fleshy. *Balanophora*. (Pf. 3¹:243.)

Order SAPINDALES. Flowers mostly actinomorphic, perfect, or diclinous; pistil 1 to several-celled, superior to inferior; ovules 1-2, erect, ascending, or pendulous; endosperm mostly 0. (Species about 2903.)

The *Sapindales* lie wholly in a phyletic side-line, and the order has been developed from some part of the intermediate order *Celastrales*, which constitutes a transition from the lower hypogynous cup flowers to those in which epigyny is fixed. In the lower *Sapindales* hypogyny still persists, but in the higher families this gives way to complete epigyny.

Family 260. **Sapindaceae**. Soapberries. Trees and shrubs, mostly tropical, with alternate (or opposite), mostly compound leaves and mostly perfect, irregular flowers; disk present or 0; petals 3-5 or 0; pistil 1-3-celled; ovules 1 or 2, ascending; endosperm usually 0. *Paullinia*, *Sapindus*, *Talisia*, *Litchi*, *Koelreuteria*, *Dodonaea*. (Pf. 3⁵:277.)

Family 261. **Hippocastanaceae**. Horsechestnuts. Trees and shrubs, with opposite, palmately compound leaves; flowers mostly regular; sepals 5; petals 4-5; stamens 8-5; pistil superior, tricarpeal; endosperm 0. *Aesculus*. (Pf. 3⁵:273.)

Family 262. **Aceraceae**. Maples. Trees and shrubs, with opposite, simple or compound leaves and small, regular flowers; sepals 4-10; petals as many or none; pistil superior, bicarpeal, winged in fruit; endosperm 0. *Acer*. (Pf. 3⁵:258.)

Family 263. **Sabiaceae**. Trees and shrubs of the tropics, with alternate, simple or compound leaves, and perfect or diclinous flowers; petals 4-5; pistil 2-3-celled; ovules 1 or 2, horizontal or pendulous; endosperm 0. *Sabia*, *Meliosma*. (Pf. 3⁵:367.)

Family 264. **Icacinaceae**. Tropical trees and shrubs, with alternate or opposite leaves and regular, perfect or diclinous flowers; sepals 5; petals 5; stamens 5; pistil superior, 1-celled, and tricarpeal; endosperm fleshy. *Icacina*. (Pf. 3⁵: 233.)

Family 265. **Melianthaceae**. Tropical trees and shrubs, with alternate leaves, and pentamerous, mostly perfect, zygomorphic flowers; endosperm fleshy. *Melanthus*. (Pf. 3⁵: 374.)

Family 266. **Empetraceae**. Heath-like shrubs, with small alternate leaves; flowers small, regular, mostly dioecious, solitary or in heads; petals present; stamens 2-3, 2-3-celled; pistil 2 to many-celled; seeds solitary, endospermous. *Corema*, *Empetrum*. (Pf. 3⁵: 123.)

Family 267. **Coriariaceae**. Shrubs with opposite, sessile leaves and perfect or diclinous flowers; 5 sepals; 5 petals; 10 stamens; 5-10 carpels, slightly united; seeds few; endosperm scanty. *Coriaria*. (Pf. 3⁵: 128.)

Family 268. **Anacardiaceae**. Sumachs. Trees and shrubs, mostly tropical, with alternate, usually compound leaves and small, perfect flowers; petals 3-7 or 0; pistil 1-5-celled, superior, but surrounded by the fleshy cup; ovules solitary, pendulous (or erect); endosperm 0. *Mangifera*, *Anacardium*, *Schinus*, *Cotinus*, *Metopium*, *Rhus*. (Pf. 3⁵: 138.)

Family 269. **Juglandaceae**. Walnuts. Trees and shrubs, with alternate, compound leaves and small, diclinous, apetalous flowers; pistil bicarpeal, 1-celled, adnate to the fleshy cup, and so inferior; ovule 1, erect, orthotropous; endosperm 0. *Engelhardtia*, *Juglans*, *Hicoria*. (Pf. 3¹: 19.)

Family 270. **Betulaceae**. Birches. Trees and shrubs, with alternate, simple leaves, and monoecious or dioecious flowers, which are in aments; petals none; calyx small or none; stamens 2-10; pistil inferior, bicarpeal, 1-2-celled; endosperm 0. *Carpinus*, *Ostrya*, *Corylus*, *Betula*, *Alnus*. (Pf. 3¹: 38.)

Family 271. **Fagaceae**. Beeches. Trees and shrubs, with alternate, simple leaves and small, diclinous flowers; petals 0; pistil mostly tricarpeal, 2-6-celled, inferior; ovules 2 in each cell, erect or pendulous; fruit usually 1-seeded; endosperm 0. *Fagus*, *Castanea*, *Pasania*, *Quercus*. (Pf. 3¹: 47.)

Family 272. **Myricaceae.** Bayberries. Shrubs and trees, with alternate, simple leaves and small, achlamydeous, diclinous flowers; petals 0; pistil free, bicarpellary, 1-celled; ovule 1, erect, orthotropous; endosperm 0. *Myrica*. (Pf. 3¹: 26.)

Family 273. **Julianaceae.** Dioecious, tropical trees, with alternate leaves; flowers small, apetalous, dioecious; stamens 4-8; pistil of 3-5 carpels; endosperm 0. *Juliana*. (Pf. Nachträge zu Teil II-IV, 335, and Syllabus, 161.) This family is given place here very doubtfully.

Family 274. **Proteaceae.** Shrubs, trees (and herbs) of the southern hemisphere, with mostly alternate, simple, usually coriaceous, evergreen leaves; flowers perfect or diclinous; sepals petaloid; petals 0; stamens 4; pistil monocarpellary, 1-celled; ovule 1, erect or pendulous; endosperm little or none. *Protea*, *Leucadendron*, *Grevillea*, *Hakea*, *Banksia*. (Pf. 3¹: 118.) This puzzling family is given place here very doubtfully.

Order UMBELLALES. Flowers actinomorphic (regular), usually perfect, 4-5-merous; calyx small to minute; stamens usually definite (4-5); pistil syncarpous, 1 to many-celled, its ovary inferior; ovules solitary, pendulous; styles free or united at the base; endosperm copious; embryo usually minute. (Species about 2809.)

Family 275. **Araliaceae.** Aralias. Trees, shrubs (and herbs), mostly tropical, with alternate leaves; flowers in umbels, heads, or panicles; ovary 2-15-celled; fruit a berry with a fleshy or dry exocarp. *Hedera*, *Aralia*, *Panax*. (Pf. 3⁸: 1.)

Family 276. **Apiaceae.** Parsleys. Herbs (shrubs and trees), with alternate leaves; flowers small, pentamerous, mostly umbellate; ovary 2-celled; fruit splitting into two dry indehiscent mericarps. *Hydrocotyle*, *Sanicula*, *Eryngium*, *Coriandrum*, *Conium*, *Apium*, *Cicuta*, *Carum*, *Foeniculum*, *Angelica*, *Ferula*, *Heracleum*, *Daucus*. (Species 2177.) (Pf. 3⁸: 63.)

Family 277. **Cornaceae.** Cornels. Shrubs and trees (rarely herbs), with usually opposite leaves; flowers larger, 4-5-

merous, umbellate, capitate, or corymbose; ovary 2-4-celled, fruit drupaceous. *Garrya*, *Nyssa*, *Cornus*, *Aucuba*. (Pf. 3^s:250.)

Super-Order COTYLOIDEAE - SYMPETALAE. Petals united. Carpels few, united, inferior; stamens usually as many as the corolla-lobes, mostly attached to the corolla.

Order RUBIALES. Flowers 4-5-merous, actinomorphic (rarely zygomorphic); stamens 4-5, attached to the corolla; calyx small; ovary 2-8-celled; ovules 2 to many in each cell. (Species about 5063.)

Family 278. **Rubiaceae**. Madders. Trees, shrubs and herbs, mostly tropical, with opposite or whorled leaves; flowers usually perfect, and regular, with valvate, contorted, or imbricate corolla-lobes; carpels mostly 2; style simple, bifid, or multifid; fruit a capsule, berry, or drupe; endosperm from fleshy to 0. *Houstonia*, *Cinchona*, *Bouvardia*, *Cephalanthus*, *Randia*, *Coffea*, *Mitchella*, *Galium*, *Rubia*. (Pf. 4⁴:1.)

Family 279. **Caprifoliaceae**. Honeysuckles. Mostly woody plants with opposite leaves; flowers usually zygomorphic, with imbricate corolla-lobes; carpels 2-5, with 1 or more pendulous ovules; style usually with a capitate undivided stigma; fruit a berry; endosperm fleshy. *Sambucus*, *Viburnum*, *Linnaea*, *Lonicera*. (Pf. 4⁴:156.)

Family 280. **Adoxaceae**. Moschatels. Slender herbs with scaly rootstocks, bearing ternately compound leaves; flowers small, regular, greenish, in heads; stamens about 10; ovary 3-5-celled; fruit drupaceous; endosperm cartilaginous. *Adoxa*. (Pf. 4⁴:170.)

Family 281. **Valerianaceae**. Valerians. Herbs (and shrubs) with opposite leaves; flowers somewhat irregular, cymose, corymbose, or solitary; stamens 1-4, the anthers free; ovary 1-3-celled, the ovules pendulous; fruit with 1 fertile cell, 1-seeded; endosperm scanty, or 0. *Valerianella*, *Fedia*, *Valeriana*. (Pf. 4⁴:172.)

Family 282. **Dipsacaceae**. Teasels. Herbs (and shrubs) with opposite or whorled leaves; flowers zygomorphic, in

involucrate heads; stamens 2-4, the anthers free; carpels 2, but pistil 1-celled; ovule 1, pendulous; endosperm scanty. *Cephalaria*, *Dipsacus*, *Scabiosa*. (Pf. 4⁴:182.)

Order CAMPANULALES. Flowers actinomorphic to zygomorphic; stamens mostly free, their anthers free or connate; ovary 1 to several-celled; ovules 1-8. (Species about 1539.)

Family 283. **Campanulaceae**. Bellflowers. Mostly milky-juiced herbs (shrubs and small trees), with alternate (or opposite) leaves; flowers regular or irregular; stamens usually 5, free, or more or less united; carpels 2-5; ovules many; endosperm fleshy. *Campanula*, *Lobelia*. (Pf. 4⁵:40.)

Family 284. **Goodeniaceae**. Mostly Australian herbs and shrubs, with alternate (or opposite) leaves; flowers usually irregular; stamens 5, free, or cohering above; ovary 2-4-celled; ovules many; endosperm fleshy. *Goodenia*, *Scaevola*, *Brunonia*. (Pf. 4⁵:70.)

Family 285. **Stylidiaceae**. Mostly Australian herbs, with tufted, radical, or scattered and sometimes crowded stem-leaves; flowers usually irregular; stamens 3-2, mostly connate with the style; ovary 2-celled, many-ovuled; endosperm fleshy. *Stylidium*, *Levenhookia*. (Pf. 4⁵:79.)

Family 286. **Calyceraceae**. South American herbs, with alternate leaves; flowers regular or irregular in involucrate heads; stamens attached to the corolla-tube, anthers free; ovary 1-celled; stigma capitate; ovule 1, pendulous; endosperm fleshy. *Boopis*, *Calycera*. (Pf. 4⁵:84.)

Order ASTERALES. Composites. Flowers actinomorphic or zygomorphic, collected into involucrate heads; calyx small, and often forming a "pappus"; stamens 5, epipetalous, mostly with their anthers connate, dehiscing introrsely; carpels 2, united, inferior, with one style which is 2-branched above; ovule one, erect, anatropous; endosperm 0. An immense order (commonly regarded as a family) of about 14,324 species, which are usually distributed among fourteen tribes, all of which are here raised to families. In the following arrangement the *Helianthaceae* are regarded as the lowest, from which the two principal phyletic lines have arisen, cul-

minating on the one hand in the *Eupatoriaceae*, and on the other in the *Lactucaceae*. (Pf. 4⁵:87.)

Family 287. **Helianthaceae**. Sunflowers. Calyx not capillary; receptacle chaffy; usually with ray flowers; mostly large and coarse plants, with leaves usually opposite. *Helianthus*, *Zinnia*, *Rudbeckia*, *Silphium*. (Species 1364.) (Pf. 4⁵:210.)

Family 288. **Ambrosiaceae**. Ragweeds. Calyx not capillary; receptacle chaffy; without ray flowers; mostly large and coarse plants, with leaves usually alternate, flowers diclinous. *Ambrosia*, *Xanthium*. (Species 74.) (Pf. 4⁵:220.)

Family 289. **Heleniaceae**. False sunflowers. Calyx not capillary; receptacle usually naked; with or without rays; anthers tailless; medium-sized plants with opposite and alternate leaves. *Helenium*, *Gaillardia*. (Species 449.) (Pf. 4⁵:251.)

Family 290. **Arctotidaceae**. Gazanias. Calyx not capillary; receptacle naked; anthers tailless. South African plants with mostly alternate leaves. *Gazania*, *Arctotis*. (Species 278.) (Pf. 4⁵:307.)

Family 291. **Calendulaceae**. Marigolds. Calyx not capillary; receptacle naked; anthers tailed. Old World plants, mostly tropical, with alternate leaves. *Calendula*. (Species 125.) (Pf. 4⁵:303.)

Family 292. **Inulaceae**. Everlastings. Calyx from bracteose to capillary; receptacle usually naked; anthers tailed; usually rayless; mostly low plants, with alternate leaves. *Inula*, *Antennaria*, *Gnaphalium*, *Helichrysum*. (Species 1580.) (Pf. 4⁵:172.)

Family 293. **Asteraceae**. Asters. Calyx from bracteose to capillary; receptacle naked; usually with rays. Medium-sized plants, with alternate leaves. *Aster*, *Solidago*, *Erigeron*, *Bellis*. (Species 1815.) (Pf. 4⁵:142.)

Family 294. **Vernoniaceae**. Ironweeds. Calyx from bracteose to capillary; receptacle naked; without rays; style branches hispidulous. Medium-sized plants, with mostly alternate leaves. *Vernonia*. (Species 788.) (Pf. 4⁵:120.)

Family 295. **Eupatoriaceae.** Blazing-stars. Calyx from bracteose to capillary; receptacle naked; without rays; style branches papillose. Medium-sized plants, with opposite and alternate leaves. *Lacinaria*, *Eupatorium*. (Species 944.) (Pf. 4⁵:131.)

Family 296. **Anthemidaceae.** Camomiles. Calyx a short crown or wanting; involucre bracts with scarious margins; receptacle chaffy or naked; usually with white ray flowers. Medium-sized plants, with alternate leaves. *Anthemis*, *Chrysanthemum*, *Artemisia*. (Species 915.) (Pf. 4⁵: 267.)

Family 297. **Senecionidaceae.** Groundsels. Calyx capillary; involucre bracts mostly 1-seriate; receptacle naked; flowers mostly yellow, with or without rays. Medium-sized to large plants, with alternate leaves. *Senecio*, *Arnica*. (Species 1982.) (Pf. 4⁵:283.)

Family 298. **Carduaceae.** Thistles. Calyx mostly capillary; involucre bracts multiseriate; anthers tailed; receptacle usually bristly (not chaffy); without rays. Mostly stout plants, with alternate leaves. *Carduus*, *Arctium*, *Cnicus*. (Species 1563.) (Pf. 4⁵:312.)

Family 299. **Mutisiaceae.** Mutisias. Calyx mostly capillary; receptacle usually naked; flowers all two-lipped. Medium to large (even woody) plants, of tropical or warm regions, with mostly alternate leaves. *Mutisia*, *Chaptalia*. (Species 550.) (Pf. 4⁵:333.)

Family 300. **Lactucaceae.** Lettuces. Calyx mostly capillary; receptacle usually naked; flowers all strap-shaped. Small to medium-sized plants, mostly with a milky juice, and with alternate leaves. *Lactuca*, *Hieracium*, *Cichorium*, *Leontodon*, (*Taraxacum*). (Species 1701.) (Pf. 4⁵:350.)

THE BOTANICAL GARDEN OF OAXACA

C. CONZATTI

Director of the Botanical Garden of Oaxaca, Mexico

I. GENERAL

At the end of the year 1909, when I was at the head of the Teachers' Normal School of the State of Oaxaca, a post which I had held since the middle of 1891, I was asked by the Ministry of Improvements, Colonization and Industry, at that time under Sr. Lic Don Olegario Molina, to assume the management of the Botanical Garden which was to be established on the grounds of the Agricultural Experiment Station of the same state. This station is situated about four kilometers from the city and had been in operation for only a few months.

Professor Don Félix Foëx, the first director of the station, was entrusted with the establishment of the Garden. He had several interviews with me; however attractive the proposition appeared to me, I could not decide to accept it. Finally, after much hesitation, I accepted the new position, and since then I have devoted myself to it entirely, even though success is doubtful; without fear of being contradicted, I can say boldly that I have been everything in the Botanical Garden, laborer, manager, topographer, landscape gardener, clerk, gardener, excursionist, and a hundred other things besides.

At the beginning of 1910 there was a general suspension for several months of the activities of the Station. As soon as the work could be resumed I devoted, with the half dozen men that I had at my command, the rest of that year and the whole of 1911 to the preliminary task of levelling, cleaning and adapting, in general, the ground for the new branch of the Station. This was a mistake; I recognize it now when it is too late. I should have insisted that the Botanical Garden, which was to be established on the grounds of the Station, be absolutely independent of the latter, or else I should have refused its management. Unfortunately, I did neither, and to this date

I deplore the consequences of such a serious lack of forethought, since, depending on the wills of others with ideas differing from mine, the Garden will never be able to prosper, or will prosper with great difficulties on account of lack of freedom.

Having finished the preliminary tasks which I had undertaken, I proceeded to make a sketch of the Garden as shown in fig. 1, which is here reproduced as approved by the authorities. As may be seen in the sketch, the Botanical Garden of Oaxaca is still in the process of formation. The tract of land assigned to it consists approximately of nine hectares, an area extensive enough to contain all the most prominent specimens of the mundane flora and all the characteristic specimens of the national flora.

Of the three valleys of the Station to the east of the Oaxaca and Ejutla Railroad, the Garden occupies the middle one, which is the one best suited for that purpose and at the same time most accessible. At the beginning it was subdivided into five departments, somewhat unequal in size, together comprising a rectangle 400 meters in length (from north to south) by 200 meters in width (from east to west); but later this area was increased by an addition of 3,000 square meters, which was annexed to the southwest corner, and again by a sixth department, semilunar in outline, comprising 5,000 square meters, annexed at the middle part of the west side. Deducting from this total area about two hectares which will be taken up by the prospective lake, walks, and lanes, there remain not more than seven hectares of land which can be utilized for the cultivation of plants.

As I have shown in a recent work, the Botanical Garden of Oaxaca is the first and only one worthy of the name in the whole of the Republic. This fact alone, signifying a positive progress, should have been sufficient to enlist the support of the authorities, as well as the public in general; but contrary to what might be expected, its existence has been, especially recently, extremely neglected. I have made this clear in the opinion expressed in my reports to the higher authorities, as may be seen from the following:

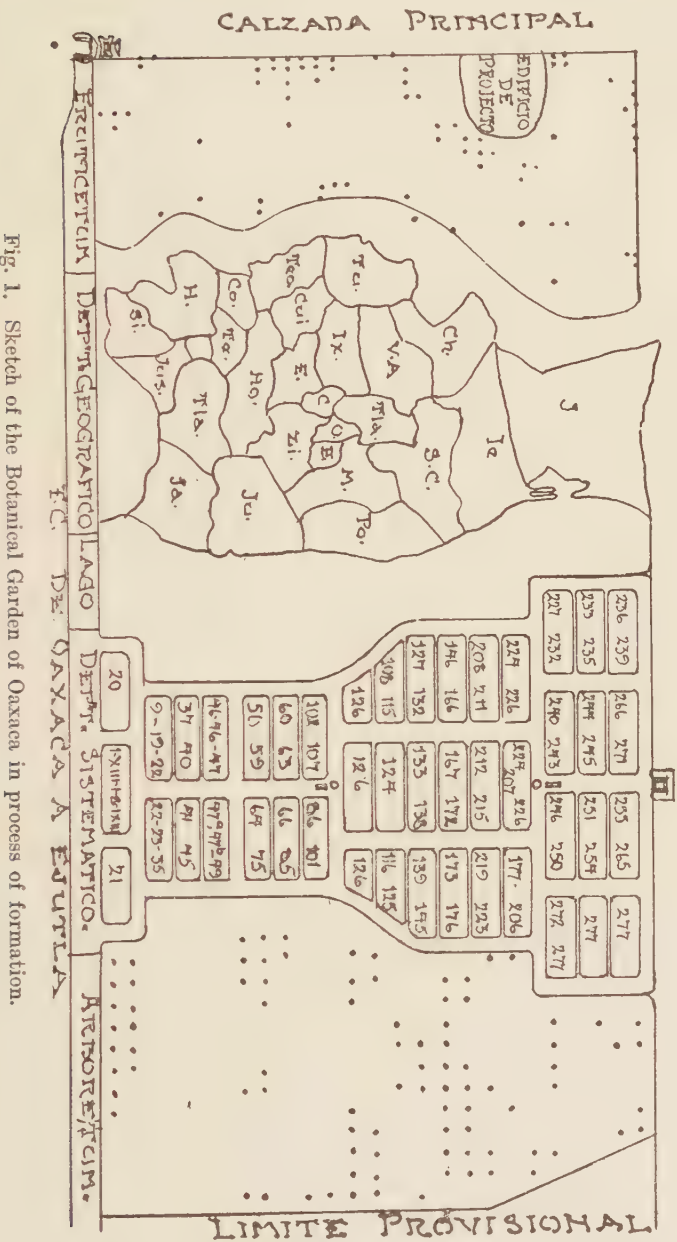


Fig. 1. Sketch of the Botanical Garden of Oaxaca in process of formation.

I am not at all satisfied with the progress of the Botanical Garden, especially during the second half of the fiscal year, 1913-1914.

Receiving no encouragement, lacking entirely means and workmen, its existence has been extremely difficult, so much so that it would be practically impossible for it to continue under the same conditions for any length of time without failing for want of support. I must not cherish any illusions in this respect, and I consider it my duty to make this clear with all frankness.'

In the same report I point out:

'Such a difficult situation is due especially to the deplorable conditions which have depleted the Public Treasury, and that as soon as the present sad state of affairs disappears (which, fortunately, seems to be already taking place), all the branches of the administration will again receive that encouragement of which they are in such great need.'

And this I believe sincerely, since I have faith in the movement which is being started for the salvation of the country and for the restoration of peace.

After all, this is the history of the development of every new idea; it is obliged to struggle on its own merits—with danger of being suppressed—against all kinds of difficulties. One of these, and certainly not the least which I have encountered, has been the predominating instability everywhere, due to the political disturbances which have been ravaging the country for a long time. This circumstance and the absolute lack of means have prevented me from making the trips which I had planned in order to bring to the Garden some living plants, which to-day constitute the most pressing need of our institution. I am convinced that the life of the Botanical Garden depends essentially on providing it with plants. Since the departments are really well prepared, the essential thing now is to fill them with plants, preferably with the greatest possible number of specimens of the Mexican flora which are found in the mountains; and the only effective way of obtaining them is to go and get them. As long as this cannot be done, the work of the Garden must be limited to the routine work of preserving what is already there.

II. DETAILED DESCRIPTION

At the end of 1913, according to the compilation made at that time, the Botanical Garden contained the following

plants: 1,099 in the systematic department, 101 in the arboretum, 1,158 in the propagation department, and 1,035 in the geographical department and the fruticetum, or a total of 3,393 specimens. For reasons already mentioned, the Botanical Garden from then until now has not only remained stationary, since it has received no appreciable additions, but it has also deteriorated a great deal, partly because a great number of plants have dried up from lack of water, and partly because its personnel—reduced to only four workmen—is insufficient to attend to the varied duties which are required. In fig. 1 some of the plants are indicated by black dots as occurring in the outer departments, arboretum and fruticetum, neither of which have any particular shape.

GEOGRAPHICAL DEPARTMENT

This department, on the contrary, is meant to represent in its main outlines the political map of the State of Oaxaca, the divisions of which are marked with the initial letters of the districts which constitute it. These districts at present are grouped, primarily on the basis of their climatic conditions, into six natural regions, as follows: Central, Cuicateca, Serana, Istmica, Costena, and Mixteca, separated from one another by lanes two meters in width. The edges of these regions have already begun to receive—as a kind of an enclosure—the typical plants of each region, while the interior of each will receive the most characteristic vegetable productions of the exuberant soil (see fig. 2).

In accordance with this plan, the central region (fig. 2), which consists of the districts (see fig. 1) E—to the right of O—(Etla), Zi (Zimatlan), M (Miahuatlan), E—to the left of C—(Ejutla), Tla (Tlacolula), and O (Ocotlan), all bordering on, or similar by their products to, district C (Center), shows now on its perimeter 121 specimens of *Ceanothus azureus*, a vigorous and elegant shrub of the hills which surround the Capitol.

The point corresponding to Santa Maria del Tule, a small village in the same region and situated about two leagues east of Oaxaca, is planted with a shrub “Sabino del Tule”

(*Taxodium distichum*) two meters in height and a direct offspring—by seed—from its historic parent. Among other things, it has the merit of being the oldest member of the department.

The Cuicateca region, consisting of the districts Cui (Cuicatlan), Teo (Teotitlan), and Tu (Tuxtepec), is limited now to 65 specimens of *Vallesia glabra*, or "Tree of the Pearls," native of the Canyon of Tomellin. This small collection is characterized by its exuberant growth and uniform size. Of the districts which constitute this region, only Cuicatlan has received a supply of plants—twenty-two different specimens from Quiotepec. Among these are six plants of *Bursera succedanea* from Linaloé, called "Palo Hediondo" (fetid stick) by the natives of that place.

Three districts form the Serrana region, Ix (Ixtilan), V. A. (Villa Alta), and Ch (Choapam); only very recently I have planted around these, 81 specimens of *Cerocarpus fothergylloides*, a beautiful rustic little tree which is native of this region.

The perimeter of the Istmica region, composed of the districts J (Juchitan) and Te (Tehuantepec), was also planted in a similar manner with some 34 specimens of an arboreal *Pereskia*, new to science, from the coast of Salina Cruz. In the district of Tehuantepec I have planted 30 plants coming from the same region and belonging to about a dozen species in several genera—*Stemmadenia*, *Pedilanthus*, *Mimosa*, etc., and in the district of Juchitan species of several genera of the *Cactaceae*—*Opuntia*, *Cereus*, *Mamillaria*, *Selenicereus*, *Echinocactus*, etc.—have been planted.

On the southern side of this department there are planted 40 palm-trees, species of *Phoenix*, about two meters high, bordering a walk which bears the name of the famous Brazilian botanist, Barbosa Rodrigues; while on the north side runs another walk, five feet wide, called "Andres Cesalpino," along the edges of which we have planted 148 specimens of *Poinciana Conzattii* Rose, brought from Tehuantepec.

Finally I shall mention the collection of Mexican agaves

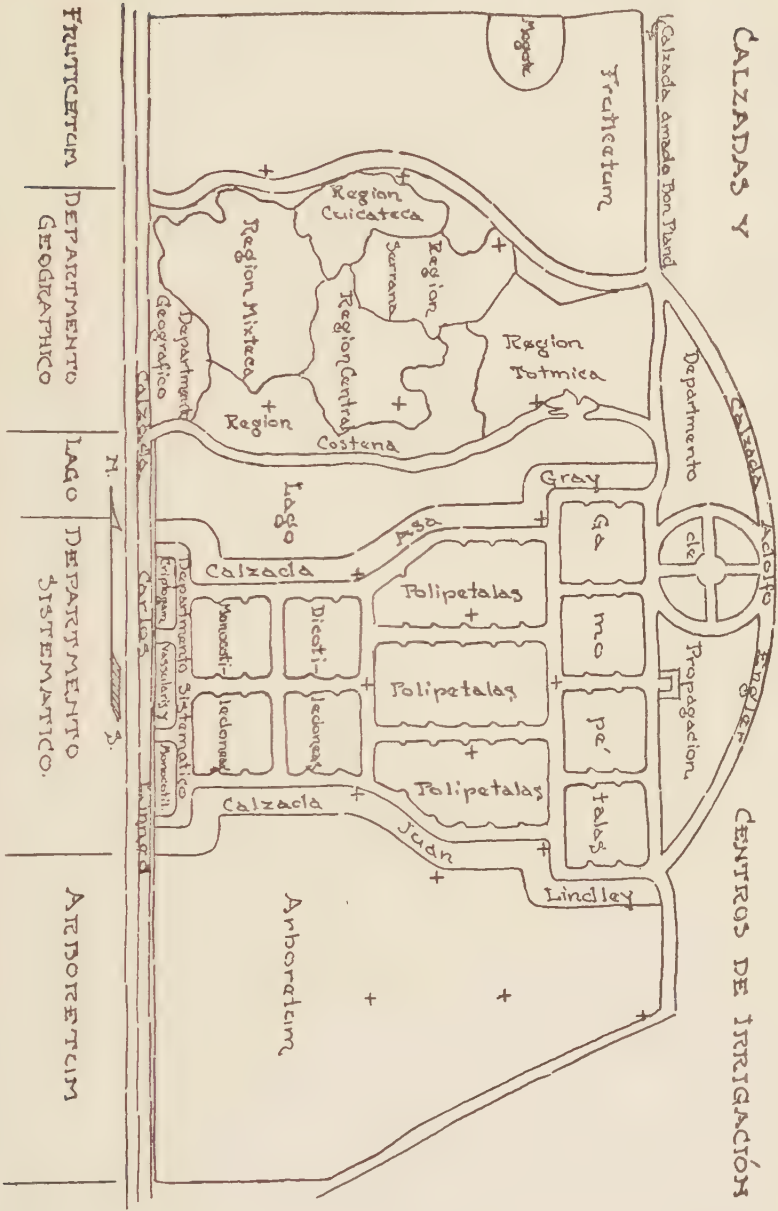


Fig. 2. Walks and irrigation centers in the Botanical Garden of Oaxaca.

which are in the district H (Huajuapam) of the Mixteca region, as well as the fact that it is planned to introduce into

this department various groups of practically useful plants—industrial, tinctorial, poisonous, medicinal, etc.

DEPARTMENT OF PROPAGATION

This department is situated in the middle eastern part of the Botanical Garden and comprises an area of not more than half a hectare. Its shape is that of a semicircle bounded on its convex side by the Adolf Engler walk; this is the name of the famous author of the classification adopted by the Garden, with few very slight exceptions suggested by the 'Lexicon Generum Phanerogamarum' of von Post and O. Kuntze. The sides of this walk are planted for the time being with various specimens of *Melia Azedarach*, but in the near future these will be replaced by specimens of "Rosa-Cacao," an imposing pyramid-like tree with horizontal and vertical branches.

As indicated by the name, this department is devoted to the propagation of plants for this Garden and similar establishments in this and other countries.

WALKS AND IRRIGATION CENTERS

Of the walks of the Garden, the one called "Carlos Linneo" forms the western boundary line of the Garden and serves it, so to speak, as a base. It is a straight line 420 meters long, running from north to south, parallel to the Oaxaca and Ejutla Railroad, and throughout its length there are, five feet apart, 84 specimens of *Casuarina stricta* about three meters in height. Two other walks worth mentioning on account of their width (10 meters) are the Asa Gray and the John Lindley walks; these run along the outer side of the systematic department and have as a border 105 laurels from India, as yet rather small.

One of the far-reaching improvements for the progress of the Botanical Garden has been the establishment of a practical irrigation system, which was first introduced at the end of 1913 and developed later as shown in fig. 2.

For this purpose we first laid under the ground 400 meters of 2½-inch pipe through the center of the Garden from the large circular tank, situated on the southern slope, to the wide

avenue leading from the Station building on the north. This was the main artery and at fixed points, which were carefully selected beforehand, crosses were placed to mark the respective connections. These consisted of lateral ramifications of smaller pipe which were to carry the water to the 35 irrigation centers, 50 meters apart, into which the Garden is subdivided.

All these centers must have nozzles, and at present there are 18 of them in working order; these are marked with crosses in fig. 2. To install them we have used 500 meters of smaller piping, so that a similar amount, if not a little more, would be required to complete the network. Of these irrigation centers eight belong to the arboretum, twelve to the systematic department, seven to the geographical department, five to the fruticetum, and three to the propagation department. As soon as the Botanical Garden has completed its irrigation system and has a sufficient supply of water for all seasons, we shall be able to consider its existence as assured.

SYSTEMATIC DEPARTMENT

Together with the two preceding departments, the geographical and propagation departments, the systematic department constitutes the central part of the Garden, and from the botanical point of view is the most interesting of them all. Many plants have already been planted in it, as may be seen in pl. 3, which represents the central part of the department; but the empty places are still numerous, and the need of having them planted is great. The shape of this department is that of an immense cup, 200 meters long and measuring 145 meters at its widest part.

As I have shown in a previous paper, which was published some time ago in the 'Memorias y Revista de la Sociedad Científica "Antonio Alzate,"' of Mexico, and to which I now refer for a better presentation of this subject, 'its interior is subdivided into 45 large squares approximately equal, among which are distributed the 277 phanerogamic families of the "Syllabus" of Dr. Engler.' The plants in this department, therefore, are arranged strictly in the order of affinity,

namely, vascular cryptogams and monocotyledons at the base, followed in order by the dicotyledonous groups, *Apetalae*, *Polypetalae*, and finally the *Gamopetalae*. With the latter the lineal series is closed, since according to the consensus of modern opinion they constitute the most highly differentiated group of flowering plants.

In the preceding lines I have endeavored to condense the most prominent features relative to the life of the Botanical Garden of Oaxaca. They are totally without pretense on my part, although they would wish to carry to the minds of all those who may read them the same high concept which I myself have formed of such a progressive institution.

In spite of the discouragement that I often feel about the Garden, I have confidence in its final success. Everything indicates that to-day the Republic is approaching rapidly a better era, which will be effected through organic peace and progress in its truest sense, since the horizon appears already free from the dark clouds.

In concluding, I wish to say that the Botanical Garden of Oaxaca, after showing itself in the preceding lines in all its smallness, has the honor of sending its older brother, the Missouri Botanical Garden of St. Louis, its most cordial congratulations for the Twenty-fifth Anniversary, wishing it long life and abundant prosperity.

EXPLANATION OF PLATE

PLATE 3

General view of the Botanical Garden of Oaxaca, Mexico, particularly of its Systematic Department.



THE ORIGIN OF MONOCOTYLEDONY

II. Monocotyledony in Grasses

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The University of Chicago

Recently Dr. Land and I published¹ the results of an investigation suggested by a specimen of *Agapanthus umbellatus*, one of the South African *Liliaceae*, possessing two good cotyledons. It seemed to us that if the seedlings of the same species are indifferently monocotyledonous or dicotyledonous, there must be some evident relationship between the two conditions. These two conditions of the seedling of *Agapanthus* were compared critically, and *Sagittaria* was included in the investigation because it has stood, along with *Alisma*, for the typical monocotyledonous embryogeny, in which the terminal cell of a filamentous proembryo is said to give rise to the single cotyledon, in contrast with the dicotyledonous embryogeny, in which the corresponding terminal cell produces the stem tip, and the cotyledons are distinctly lateral. No contrast would seem sharper and less capable of being confused with intergrades.

The result of the investigation, as recorded in the paper referred to, was to show us that there are no such rigid categories for cotyledony; that the cotyledonary apparatus is always the same structure, arising in the same way, and varying only in the details of its final expression. Briefly stated, the situation is as follows: In the embryogeny of both monocotyledons and dicotyledons, a peripheral cotyledonary zone gives rise to two or more growing points, or primordia; this is followed by zonal development, resulting in a cotyledonary ring or sheath of varying length. If both growing points con-

¹ Coulter, John M., and Land, W. J. G. The origin of monocotyledony. *Bot. Gaz.* 57: 509-519. *pl.* 28-29. 1914.

tinue to develop equally, the dicotyledonous condition is attained; if one of the growing points ceases to develop, the continued growth of the whole cotyledonary zone is associated with that of the other growing point, and the monocotyledonous condition is attained. In like manner, polycotyledony is simply the appearance and continued development of more than two growing points on the cotyledonary ring. It follows that cotyledons are always lateral structures, arising from the peripheral zone developed at the top of a more or less massive proembryo. This reduces cotyledony in general to a common basis in origin, the number of cotyledons being a secondary feature. The constancy in the number of cotyledons in a great group is no more to be wondered at than the same constancy in the number of petals developed by the petaliferous zone. This is a brief statement of the thesis of our previous paper, detached from the evidence upon which it was based.

It was our purpose to extend the investigation far enough to include all of the representative regions of monocotyledons, so that the conclusion could be tested sufficiently to lead either to its abandonment or to its establishment. This second paper deals with a study of the embryos of grasses, which have been examined more extensively, perhaps, than the embryos of any other monocotyledonous group. As a result of this extensive study there are available many accurate records in the form of good figures, giving the details of embryogeny in such a way that interpretation is almost as satisfactory as it would be from the actual material. Of course this use of illustrations has been checked by the direct inspection of more or less material.

The embryo of grasses early attracted special attention because it does not seem to conform to the plan of the ordinary monocotyledonous embryo. Certain structures appear that could not be accounted for, but they enriched terminology. As a consequence, the nature of scutellum, epiblast, and coleoptile became subjects of discussion. It was to be expected that

the embryo of grasses, with all of its unusual structures, would be interpreted in terms of a rigid conception of the monocotyledonous embryo; in other words, that the conventional monocotyledonous embryo would be read into the grass embryo. There is no better illustration of the compelling power of a preconception than this treatment of the grass embryos, for it so happens that they show all the intermediate stages between dicotyledony and monocotyledony.

Very early in the history of this subject, the scutellum came to be recognized as a cotyledon. The corollary to this proposition, however, was that it must be recognized also as a terminal structure. Any one who has seen the vascular system of the embryo of corn (fig. 1), the most highly specialized of all grass embryos, with its distinct axial cylinder, made up of stem cylinder and hypocotyl cylinder, and the cotyledonary strands leading off from the intermediate cotyledonary plate, just as do the strands of any lateral cotyledons, will understand the great difficulties in the way of interpreting this cotyledon as a terminal structure.



Fig. 2. Embryo of *Zizania aquatica*: s, scutellum; e, epiblast; c, coleoptile; $\times 11$. — After Bruns.



Fig. 1. Embryo of *Zea Mays*: s, scutellum; c, coleoptile; the vascular cylinder of the embryo is shown, made up of stem cylinder and hypocotyl cylinder, also the lateral origin of the cotyledon (scutellum) from the cotyledonary vascular plate; opposite the vascular connection of the cotyledon there appears a group of procambium cells, marking the origin of another cotyledonary strand connected with the suppressed second cotyledon (epiblast); $\times 18$.

The structure which presented the greatest difficulty, however, was the epiblast, usually defined as a small scale "opposite" or "over against" the

cotyledon. The definition is accurate, for the epiblast occupies exactly the place of a second cotyledon opposite the large and

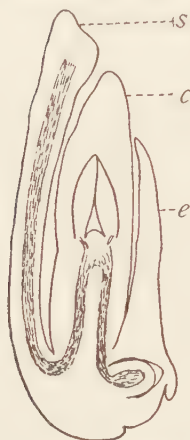


Fig. 3. Embryo of *Leersia clandestina*: s, scutellum; e, epiblast; c, coleoptile; $\times 44$. — After Bruns.

functional one (fig. 2). If some one had found an epiblast vigorous enough to establish vascular connections, this debated structure would long since have been accepted as a second cotyledon, for the definition of it always emphasized the fact that it is a scale in the right position for a cotyledon, but with "no vascular strands."

So obvious is the interpretation of the grass embryo when an epiblast is developed that Porteau in 1808, Mirbel in 1809, Turpin in 1819, and Bischoff in 1834, all called the epiblast a rudimentary cotyledon. The submergence of this idea seems to have been due to Schleiden, who in 1837 dissented from this view, and it disappeared from literature. It reappeared in 1897, when Van Tieghem, in his paper on the embryo of grasses and sedges,¹ reiterated it, based chiefly upon the study of vascular connections.

Any series of sections, cross or longitudinal, through the embryos of grasses, shows the following facts: the so-called scutellum or functional cotyledon arising from the peripheral cotyledonary ring or sheath which surrounds the apex of the embryo, and establishing vascular connections laterally with the cotyledonary plate; the epiblast in a similar relation to the cotyledonary ring on the opposite side, and varying in development from a structure somewhat smaller than the large cotyledon, to complete suppression; and the apex of the



Fig. 4. Embryo of *Oryza sativa*: s, scutellum; e, epiblast; c, coleoptile; $\times 22$. — After Bruns.

¹ Van Tieghem, Ph. Morphologie de l'embryon et de la plantule chez les Graminées et les Cypéracées. Ann. d. Sci. Nat., Bot. VIII. 3: 259-309. pl. 14-16. 1897.

embryo, continuing beyond the cotyledonary ring or sheath, and producing a variable number of leaves.

The early appearance and rapid development of these leaves seems to account for the abortion of one of the growing points. I am convinced that if grass embryos had been the only monocotyledonous embryos studied, we should never have heard of terminal cotyledons.

Some common grasses, whose embryos have been figured by Bruns,¹ may be used to illustrate stages in the abortion of the second cotyledon. The abortion always is

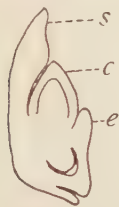


Fig. 6. Embryo of *Leptochloa arabica*: s, scutellum; e, epiblast; c, coleoptile; $\times 44$. — After Bruns.

accompanied by the diversion of the growth of the whole cotyledonary zone in connection with the growing point that remains active; so that growing tissue is not suppressed, but develops as one structure rather than as two.

In *Zizania aquatica* (fig. 2), the so-called epiblast is very conspicuous, arising as distinctly from the peripheral cotyledonary ring as does the so-called scutellum, and attaining at least one-quarter to one-third of its length. This unusual development of the second cotyledon is associated with the fact that the stem axis above the cotyledons develops a long internode, so that the first leaves begin to appear at an unusual distance from the origin of the cotyledons. In fact, in this case the length of the second cotyledon is approximately the length of the first internode, and where the leaves begin this cotyledon ends.

In *Leersia clandestina* (fig. 3), the second cotyledon (epiblast) approaches the large cotyledon in length even more



Fig. 5. Embryo of *Spartina cynosuroides*: s, scutellum; e, epiblast; c, coleoptile; $\times 13$. — After Bruns.



Fig. 7. Embryo of *Triticum vulgare*: s, scutellum; e, epiblast; c, coleoptile; $\times 22$. — After Bruns.

¹ Bruns, Erich, Der Grasembryo. Flora 76: 1-33. pl. 1-2. 1892.

than does that of *Zizania*, and all the connections of the various organs show a lateral origin for the cotyledons, and a terminal origin for the "coleoptile," a structure made up chiefly of leaves arising from an indistinctly differentiated stem-tip region.

Oryza sativa (fig. 4) is interesting in the relation of the parts of the embryo, the "scutellum" and "epiblast" being opposite and well-balanced structures, between which the prominent plumule (a name expressing the real character of the "coleoptile") is evident.

Fig. 8. Transverse section through cotyledon (*s*), showing it embracing the plumule (*c*) of *Zea Mays*: the plumule shows three distinct leaves and the terminal stem tip; the succession of opposite vascular bundles indicates that a bundle opposite that of the cotyledon is missing, but its rudiment is evident in a lower section; $\times 20$.

relation to the functioning cotyledon, and the relation of both to the plumule are evident.

In *Leptochloa arabica* (fig. 6) and in *Triticum vulgare* (fig. 7), the epiblast remains very small, but the significant connections are evident.

It is in the embryo of *Zea Mays* that this reduction series reaches its extreme expression in the complete disappearance of the epiblast or second cotyledon (fig. 1), whose position is indicated merely by more or less protuberant

In *Spartina cynosuroides* (fig. 5), the small cotyledon (epiblast) is less prominent, but its

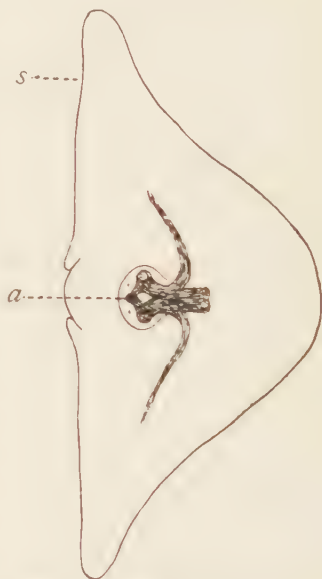


Fig. 9. Transverse section through the cotyledonary plate of *Zea Mays*: the functioning cotyledon (*s*) does not overlap a small protuberance, which represents the site of the missing cotyledon (epiblast), as indicated also by the appearance of a procambium mass (*a*), which is the rudiment of a former vascular connection; $\times 20$.

tissue and by the very obvious vascular relations. A cross-section of this very specialized embryo is instructive (figs. 8 and 9). The large functional cotyledon is seen originating on one side, embracing the vascular axis of the embryo and more or less overlapping the other side, where in most grasses the second cotyledon (epiblast) appears. Moreover, in the section of the centrally placed plumule, with its succession of leaves, a section of the stem tip may be seen, clearly representing the axis of the embryo, with no suggestion of a lateral origin. A transverse section through the cotyledonary plate (fig. 9) shows some tissue developed at the site of the missing cotyledon (not overlapped by the functioning cotyledon). This is emphasized by the appearance of a mass of procambium at the base of the protuberance, which in other grasses develops into the epiblast. This procambium is distinctly a rudiment of a former vascular connection.

Some idea of the frequency with which the second cotyledon appears among the grasses may be obtained from the excellent work of Bruns on the grass embryo, published in 1882, and from the work of Van Tieghem, already cited, published in 1897. Bruns examined 82 genera, representing 12 tribes. In 29 of these genera epiblasts were present, and the genera represented 9 of the 12 tribes. The tribes in which no epiblasts were found were *Oryzeae*, *Agrostideae*, and *Aveneae*. The situation in the *Agrostideae* is noteworthy, for 13 genera were examined, and no trace of an epiblast found. *Festuceae* may be mentioned, for 20 of its genera were examined, and only 4 of them were found to possess epiblasts. Taking Bruns' results as a whole, they indicate that approximately 40 per cent of the grasses still develop a second cotyledon to a stage that enables it to be recognized under ordinary inspection as a definite structure.

The work of Van Tieghem included a somewhat wider range of forms, 91 genera being examined, and 61 of these showed epiblasts. This suggests that perhaps in as many as two-thirds of the grasses a second cotyledon is more or less obvious. In any event, it is certain that the grasses as a whole exhibit a remarkable number of transition stages from dicoty-

ledony to monocotyledony; and this fact strongly supports the view that grasses are a comparatively primitive assemblage of monocotyledons.

It is not difficult to explain the prolonged misconception concerning monocotyledony. When the first detailed studies of monocotyledonous embryogeny were made by Hanstein, and supplemented by Famintzin, a form (*Alisma*) with a filamentous proembryo was selected. If a form with a massive proembryo had been selected for these early investigations, there would probably have been no misconception, for in such proembryos the peripheral (that is, lateral) cotyledonary zone is so evident that it could hardly have escaped recognition. Since that time, embryogeny that starts with a filamentous proembryo has been regarded as the typical embryogeny, and all other kinds of proembryos have been dismissed as exceptions. In the case of this filamentous proembryo, it was observed that the terminal cell passed into the quadrant and octant stages, and later a terminal cotyledon appeared. It seemed safe to conclude that the terminal cell had developed the terminal cotyledon. The inference was true so far as it went, but it failed to recognize the fact that the terminal cell develops other structures as well. With the origin of the terminal cotyledon disposed of, the conclusion was confirmed by the appearance at its base of a notch, from which arose the stem tip. What could be more obvious than that the stem tip is lateral in origin, and therefore must arise from the cell of the proembryo behind the terminal one? In this way the conventional embryogeny of monocotyledons was established, and the relation of monocotyledony to dicotyledony became completely obscured.

The facts not observed in these earlier investigations are as follows: The terminal cell of the proembryo forms a group of cells; the peripheral cells of this group develop the cotyledonary ring or sheath, on which two growing points appear. One of these growing points soon ceases to be active, and the whole zone develops in connection with the other growing point; but at the base of the growing cotyledon a notch is left by the checking of the other growing point. This notch

is really the space between the two very unequal cotyledons, which surround the real apex of the embryo. The apex of the embryo is at the bottom of the notch, and not at the tip of the large embryo. This apex soon begins to form leaves, and the so-called stem tip appears issuing from the bottom of the notch, in a relation apparently lateral only because the two cotyledons are so unequal. Furthermore, when the stem tip is examined, it is found not to be a stem tip, but a cluster of leaves whose rapid development has aborted one of the growing points on the cotyledonary zone. All this is very obvious in grasses, and is equally obvious in any massive proembryo, but it escaped the earlier observers of filamentous proembryos.

The general conclusion is that monocotyledony is simply one expression of a process common to all cotyledony, gradually derived from dicotyledony, and involving no abrupt transfer of a lateral structure to a terminal origin.

This paper was prepared in collaboration with Dr. W. J. G. Land, who also supplied the material and made the illustrations.

THE HISTORY AND FUNCTIONS OF BOTANIC GARDENS

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There are three things which have stimulated men throughout the ages to travel far and wide over the surface of the globe, and these are gold, spices and drugs. It is to the two latter of these universal needs of man that we may trace the origin and foundation of botanic gardens.

The value of spices has led to the foundation of more than one botanic garden in the tropics, while to the necessity for drugs must be attributed the formation of the earliest botanic gardens in Europe.

Before entering more fully into the history of the founding of the various botanic gardens it may be pointed out that progress in the science of botany and the establishment of gardens were by no means contemporaneous. To the Greeks, for instance, we owe the foundation of our knowledge of the classification of plants, and these early botanists were assiduous in collecting plants from all available sources and in drawing up accurate descriptions.

Little interest, however, would appear to have been aroused in them to cultivate the plants they so carefully described, and the only record we have of the existence of anything of the nature of a botanic garden is the mention of Aristotle's Garden at Athens which he bequeathed to Theophrastus, by whom it was newly equipped and improved.

Prior to the interest displayed by the Greeks in the vegetation of the earth and quite independent of their influence we find evidence of the formation of gardens in Egypt, Assyria, China, and subsequently in Mexico—gardens not strictly botanic in our more modern sense but enclosures¹ set apart

¹ See Greene, E. L. Landmarks of botanical history. Smithsonian Misc. Coll. 54: pp. 56–57. 1909. No doubt Theophrastus (370–286 or 262 B. C.) gained his intimate knowledge of plants very largely from the specimens cultivated in this early Athenian garden.

for the cultivation of plants of some definite economic or aesthetic value.

In considering the history of this subject we look back to the earliest history of mankind, with which gardening in some form is inseparably connected, for, as Francis Bacon reminds us:

"God Almighty first planted a Garden and indeed it is the Purest of Humane Pleasures. It is the greatest refreshment to the spirits of man; without which Buildings and Palaces are but grosse Handyworkes: and a man shall ever see that when ages grow to civility and elegancie men come to Build stately sooner than to garden finely as if gardening were the greater Perfection."

We are still exercised to seek out and grow "every tree that is pleasant to the sight and good for food," and the "tree of life" also in the midst of the garden is ever the object of our inquiries. It would be well indeed if at this present time we could discover that tree whose leaves were to be "for the healing of the Nations."

The earliest garden of which we have any representation is the Royal Garden of Thotmes III of about the year 1000 B. C., which was planned by Nekht, head gardener of the gardens attached to the Temple of Karnak.¹ This Royal Garden, rectangular in outline, with its rows of date and branched doum palms and with its vine pergola and lotus tanks, was probably in the nature of a pleasure garden, while those attached to the temples may well have been of more economic importance. The Chinese,² however, should, as might be supposed, be credited with being the real founders of the idea of botanic gardens, since it is clear that collectors were despatched to distant parts and the plants brought back were cultivated for their economic or medicinal value. The semi-mythical Emperor Shen Nung, of the twenty-eighth century B. C., is considered to be the Father of Medicine and Husbandry and is said to have tested the medical qualities of herbs and discovered medicines to cure diseases. If this be

¹ See Holmes, E. M. Horticulture in relation to medicine. Roy. Hort. Soc., Jour. 31: pp. 44-45. *f.* 11. 1906.

² Bretschneider, E. Botanicon sinicum. China Branch Roy. Asiatic Soc., Jour. N. S. 25: p. 24. 1893.

correct, it was but a repetition of history which led to the foundation of the monastic herb gardens in the ninth century A. D., and the subsequent institution of botanic or herb gardens in connection with the medical faculties of the earliest European universities.

We learn from Bretschneider also that the Han Emperor Wu Ti (140–86 B. C.) planted a number of rare herbaceous plants and trees brought from the southern regions in the garden of his palace and the following plants have been identified from the list enumerated: *Nephelium Litchi*, *N. logan*, *Areca Catechu*, the banana, *Quisqualis indica*, *Canarium album*, *C. Pimela*, *Cinnamomum Cassia*, *Canna indica*, and sweet oranges. He also despatched officers to the north-western frontiers of China, who brought back reports on the productions of this region. Ancient Chinese authors ascribe to Wu Ti the introduction of the vine, pomegranate, safflower, common bean, cucumber, lucerne, coriander, walnut, etc.

It is a fact of no small interest in this connection to remember that the modern world has turned to China and that her vast botanical treasures have only recently been seriously explored through the enterprise of British, French, and American botanists for the enrichment of our botanic gardens and pleasure grounds.

The establishment of gardens in Mexico is a noteworthy fact—though we have but little information about them—since their origin must have been autochthonous and independent of such institutions in the Old World. Prescott¹ tells us, and we have reason to believe his account to be true, that Montezuma had extensive gardens filled with fragrant shrubs and flowers and especially with medicinal plants. New Spain, indeed, furnished more important species of medicinal plants perhaps than any other part of the world, and their virtues were understood by the Aztecs, who are credited with having studied medical botany as a science. The gardens at Iztapalan² and Chalco³ are said to have been stocked with

¹ Prescott, W. H. *Conquest of Mexico* 2: pp. 110, 111. 1847. [3rd ed. London.]

² *Ibid.* pp. 60 and 61.

³ *Ibid.* 3: p. 37. 1847; Clavigero, D. F. S. *Stor. del Messico* 2: p. 153.

trees and plants scientifically arranged, and the gardens at Chalco, which were preserved after the Conquest, furnished Hernandez with many of the specimens described in his book.¹

The cases cited, however, have little more than an academic interest for us and have in no way influenced the foundation of modern botanic gardens. These we can trace back to monastic institutions and probably to the famous injunctions of Charlemagne,² the direct outcome of which was the establishment, among others, in the ninth century, of the "hortus" at St. Gall with the attendant "herbularis," or Physic Garden, this latter being the precursor of the physic gardens established in connection with the medical faculties of the Italian and other universities in the sixteenth century.

It is fortunate that we have preserved to us exact details of the "hortus" and "herbularis" at St. Gall, with lists of the plants cultivated therein.³ The hortus was an oblong enclosure containing eighteen rectangular beds, while the Physic Garden, or herbularis (see fig. 1), formed a square set with similar beds and having the doctor's house close at hand.

The monks being bound to live on pulse, vegetables and fruits and to gather the same for themselves, the garden and its cultivation were of especial importance in the monastery. To the fostering care of the monks and to their knowledge of drugs, horticulture and botany, in common with other arts and sciences, we owe a debt the magnitude of which it is difficult to estimate.

We do well to recall at this point the services rendered in recent years to the biological sciences by the labors of Gregor Mendel in the monastic garden at Brunn, if only to emphasize how widespread and far-reaching are the functions involved in the true idea of the botanic garden.

The fourteenth and fifteenth centuries, as is well known, were times of a great revival and interest in learning, and

¹ Hernandez, F. *Nova plantarum animalium et mineralium Mexicanorum historia*. Rome, 1651.

² Holmes, E. M. *Horticulture in relation to medicine*. Roy. Hort. Soc., Jour. 31: p. 50. 1906.

³ *Archaeological Inst., Jour.* 5: p. 113; see also Amherst, A. *History of gardening in England* p. 5. 1896. [2nd ed.]

the science of botany received its due share of attention. Unfortunately, energy was chiefly employed in attempting to identify the plants named by the Greek writers with those of Western Europe and progress in the science was only fitful. The compilation of herbals was the main occupation

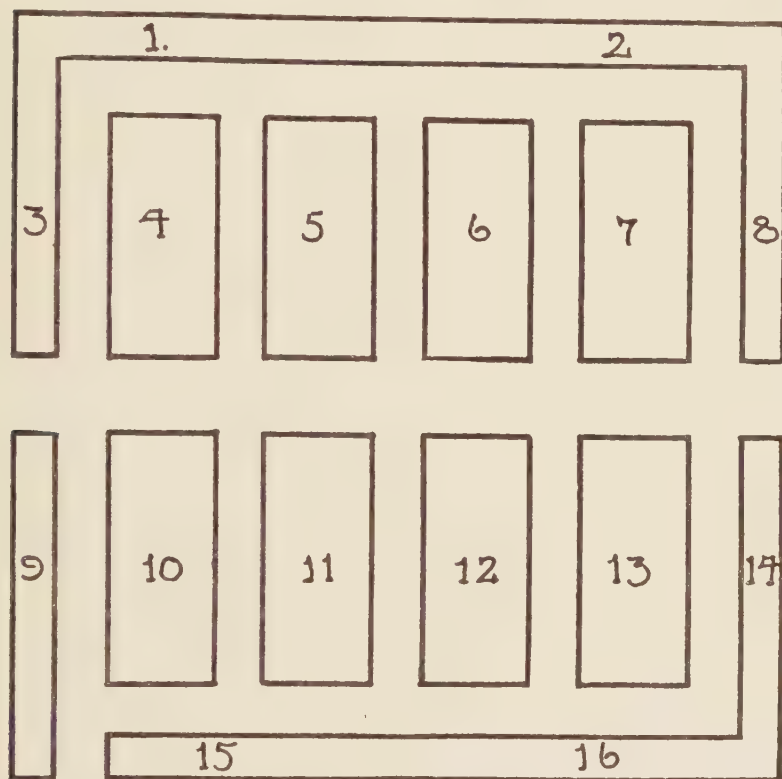


Fig. 1. Monastery of St. Gall. Physic Garden: 1, Fasiolo; 2, Sataragia; 3, Rosas; 4, Sisimbria; 5, Cumino; 6, Lubestico; 7, Feniculum; 8, Costo; 9, Lilium; 10, Salvia; 11, Ruta; 12, Gladiola; 13, Pulegium; 14, Fenugraeca; 15, Mentha; 16, Rosmarino. The Cemetery contained apples, pears, peaches, mulberries, plums, laurels, figs, hazelnuts, service, chestnuts, medlars, quinces, almonds, and walnuts.

of industrious botanists and many of these works, though of little botanical value to-day, can be treasured by us as store-houses of artistic beauty.

With the real growth in the knowledge of plants and their uses there grew up also a mass of superstitious information,

partly founded on old tradition, increased with the importation of strange drugs,¹ and partly no doubt invented by the herbalists and drug-sellers to prevent any infringement of their monopoly in plants of real or supposed medicinal virtue, and to frighten the ignorant from attempting to collect the plants for themselves.

The faint resemblance of the mandrake root to the human form, for instance, probably suggested its use as a remedy for sterility; it is still sold to-day in Egypt as a charm. Its use may have led to the discovery of its anaesthetic qualities since it was used in ancient times for this purpose, and the legends which abounded as to the danger of death to those who gathered the root may have been circulated in order to try to prevent its use for criminal purposes.

It was largely owing to the need of protecting the doctor and apothecary against the drug-sellers that the growing of "simples" in recognized gardens had its origin. As the seats of the medical profession were established in the universities and monasteries, these institutions set apart definite enclosures for the cultivation of medicinal herbs, the "simplicia" or "simples" from which the "remedia composita" were prepared by the apothecaries.

Since the universities and monasteries were generally situated in towns, their physic gardens were usually small, and on the continent of Europe we still see these ancient gardens, which have been gradually transformed into the botanic gardens of the universities.

In connection with the growth of learning and increase of observation which is noticeable in the arts and sciences at this time of renaissance, it is strange that biology was still so largely under the thrall of superstition and curious invention. Reference to the early herbals, such as the 'Buch der Natur' (1475), the 'Herbal of Apuleius' (1484), and the 'Grant Herbar' (1526), shows both as regards text and illustration a persistent state of ignorance of facts, which could easily have been remedied by observation, and possibly does not represent

¹ Medicinal plants were imported from the Continent in a dry state, hence the English word "drug," which is part of the Anglo-Saxon verb "drigan," to dry.

the true state of the knowledge of the more competent medical botanists of the period. The herbal of Brunfels (1530), with its beautiful and accurate illustrations but indifferent text, and those of Bock, Fuchs, Cordus, and many others, may be taken as evidence of the rapid advance that was taking place in the knowledge of plants, though the fabulous and mythical still found adherents even amongst the most learned.

Private physic gardens, as distinct from the monastic herb-aries, existed towards the end of the fifteenth century, and some of these developed into municipal gardens for the growing of "simples." The botanic garden at Padua, which appears to have been one of the earliest of these gardens, was founded in 1545 on the exact spot which it now occupies near the church of S. Antonio and S. Giustino. The garden owes its origin to the sound suggestion put forward at the end of the year 1542 by Francesco Bonafede, who in 1533 had founded the chair of "simples" (*Lectura Simplicium*)—the first in Europe—at the University of Padua.

This garden is of especial interest, as not only have we an excellent account of it written by de Visiani,¹ but also because it is preserved very largely in its original condition. The circular wall by which it is enclosed, though not the original one built in 1551, occupies the same site, and was rebuilt between 1700 and 1707; within the wall the garden is laid out in numerous little beds with stone edgings. The garden underwent many vicissitudes and fell into considerable decay, but in the year 1837 it was thoroughly restored, and the arrangement of the beds may well be a restoration of the original condition of the garden. In any case it affords an excellent example of the type of geometrical garden illustrated in horticultural books published at the end of the sixteenth and beginning of the seventeenth centuries,² which for so long a time dominated garden design on the Continent.

¹ de Visiani, R. *Dell' origine ed anzianita dell' orto botanico di Padova*. Padua, 1839. Saccardo, P. A. *L'orto botanico di Padova nel 1895. pl. 1-8. f. 1*. Padua, 1895.

² See illustrations of the gardens of De Vries, 1580-1583, reproduced by Sir F. Crisp in 'Illustrations of some mediaeval gardens,' 1914; and cf. Mariani, *Florilegium renovatum et auctum*. Frankfurt, 1641.

It is to be regretted that the principal features have been somewhat obscured by the growth of trees, but the ground plan fortunately remains unaltered. Pisa in 1544, Bologna in 1547, and others,¹ quickly followed the lead given by Padua. We are fortunate in possessing an elaborate plan of the Pisan garden published in Tilli's catalogue² of 1723 with a list of the plants cultivated in the various beds and enclosures, the latter being here reproduced.

EXPLICATIO
PROSPECTUS
HORTI PISANI

1. Topiarium magnum instar Tentorii, Cupressinis Arboribus flexilibus, & ferreis catenis circumdatum.
2. Umbraculum primum venustum, opere topiario, Citris Arboribus, ac Citroidibus poma suaveolentia ferentibus instructum, & fontibus ornatum.
3. Umbraculum alterum Citroidibus Florentinis repletum.
4. Vaporarium pro Plantis Americanis.
5. Vaporarium gestatorium.
6. Locus pro Plantis Aegyptiis aquam respuentibus.
7. Vaporarium cum laminis vitreis fixum ad semina vegetanda.
8. Paries per totam longitudinem Aurantiorum Olyssipponensium, aliarumque: Arborum poma sustinens.
9. Fenestrae Hypocausti.
10. Fenestrae Hybernaculi.
11. Platea cum variis Aloës Plantis.
12. Nemus exoticarum, & indigenarum Arborum.
13. Hydrophylacia, seu Castella.
14. Locus pro Plantis montanis, & Sylvestribus.
15. Laboratorii Chimici, in quo Anthlia Pneumatica reperitur, pars externa Hortum respiciens. Supra verò extat infundibulum ad pluviam recipiendam, de qua fusè D. G. Derham in suis transactionibus, ac etiam in Demonstr. cap. iii. pag. 23. mentionem facit; eadem pars externa variis fontibus, ac lapidibus figuratis est ornata; ibi scilicet reperiuntur Astroites, qui in Metallotheca Mercati pag. 235. & Corallites, Placentae, Lapis Lumbricatus cap. 55. quorum etiam aliqui sunt Lapides Cerebriformes, an huc allati sint ex Sicilia, vel Sardinia, aut ex Jamaica, ut Rayus Hist. Tom. iii. pag. 5. ex Sloanis verbis, adhuc nescimus.

¹ Botanic gardens were founded in Zurich, 1560; Bologna, 1568; Leyden, 1577; Leipzig, 1579; Montpellier, 1598; Paris, 1597, known as Jardin des Plantes after 1635; Heidelberg, before 1600; Giessen, 1605; Strasburg, 1620; Oxford, 1621; Jena, 1629; Upsala, 1657; Chelsea, 1673; Berlin, 1679; Edinburgh, 1680; Amsterdam, 1682. See also foot-note, p. 209.

² Tilli, M. A. Catalogus plantarum Horti Pisani. Florence, 1723.

16. Pergulae Laurorum.
17. Prunorum diversae Arbores murum tegentes.
18. Aurantiorum Arbores.
 Divisiones Plantarum secundum earum
 propriam naturam, areolis
 contentarum.
19. Locus Herbis tantum Hortensibus repletus.
20. Locus Acanaceis Plantis.
21. Locus Plantis Umbelliferis.
22. Locus Plantis Palustribus.
23. Locus Plantis Venenatis.
24. Locus Plantis Odoratis.
25. Locus Plantis Bulbosis.
26. Florilegii locus.
27. Vaporarium fixum, ac fimo equino repletum, ubi Ananas, &
 similes Plantae exoticae aluntur.
28. Ostium primum.
29. Ostium Laboratorii Chimici, ubi Anthlia reperitur, aditum
 respiciens.¹
30. Ostium alterum Horti publici: intus insignium Botani-
 corum Virorum effigies visuntur.
31. In Tecto Infundibulum pluviam recipiens.
32. Paries Aurantiis Hermaphroditis ornata.
33. Platea.
34. Ubi Muscae odoratae D. Chimentelli oriuntur.
35. Aditus qui ad ostium Viae publicae ducit: ibi Balenae, &
 Physeteris ossa suspensa, ut pagina 4. hujus Catalogi, ubi de
 Agarico agitur.
36. Fenestrae Domus Custodis.
37. Fenestrae Musei In earum medio Inscriptio haec legitur.

The beds at Pisa are arranged on the geometrical plan and the picture of the garden shows a perfect specimen of the typical formal garden of the end of the sixteenth century. The plants were grouped chiefly according to their properties and morphological characteristics: Thus one finds beds for poisonous plants, prickly plants, smelling plants, bulbs and marsh plants. "Aloes" (*Aloe*, *Gasteria*, etc.) were also grown and are figured in the catalogue and there was a "vaporarium pro plantis Americanis."

The lectures on "simples" delivered at the early Italian universities were not at first accompanied by demonstrations upon living specimens, but the growing of the plants in

¹ This and the remaining buildings, etc., are shown on a separate plan which is not reproduced here.

definite gardens led to the establishment of demonstrations upon living specimens of the medicinal plants, and at Padua sixteen years after the foundation of the garden, a separation was made of the "Lectura" from the "Ostensio simplicium," or demonstration of living plants.

Botany, however, in all these early universities to which gardens were attached was merely ancillary to medicine. At Montpellier, for instance, the same professor taught anatomy in winter and botany in summer, and as late as 1773 anatomy, surgery and botany formed the subjects for one and the same professor at Jena.

Very soon after the founding of the gardens at Padua and Pisa, plants other than those of strictly medicinal value were introduced into the physic gardens. This was due to the revival of interest in the plant world which took place about the middle of the sixteenth century and to the desire for travelling and interest in collecting which then sprang up. Conrad Gesner, writing in 1561 in the 'Horti Germaniae,'¹ mentions that in botanic gardens not only medicinal herbs were cultivated but also other plants, especially rare ones, for the purpose of observing and admiring nature:

"Hortorum alii vulgares sunt, utilitatis tantum gratia confiti: in quibus olera, legumina, vites, fructus qui edendo sint, & gramen, usum homini aut pecori praebent. Alii medicinales, ut Medicorum & Pharmacopolarum: in quibus non hortenses tantum stirpes, sed etiam sylvestres omnis generis, & peregrinae quoque coluntur, propter remedia quae ex ipsis earumve partibus homini fiunt. Alii similes istis, sed magis varii, in quibus non solum plantae remediis nobiles, sed aliae etiam quae vis rariores praesertim coluntur, propter admirationem & contemplationem naturae."

John Ray visited both Padua and Pisa early in 1664; referring to the garden at Padua, he says: "Here is a public Physick garden, well stored with simples but more noted for its precepts, men eminent for their skill in Botanies." The Pisan garden at this time would not appear to have been in a very flourishing condition since Ray merely remarks, "*The*

¹ Gesner, Conrad. *Horti Germaniae* p. 237 verso. Strasburg, 1561.

Physick Garden at our being there but meanly stored with simples."¹

In particular, Gesner² alludes to several gardens at Padua and mentions the one under the charge of Anguillara, which was no doubt the Botanic Garden, as having a fine collection of plants with representatives from Syria, Crete and other distant places. He refers in the first place to the Garden of Caspar à Gabrielis "vir inter nobiles Patavinos longe nobilissimus," and then to "Priulanus hortus magnificus," which was under Aloisius Anguillara (Romanus). Gesner's account is as follows:

"Ibidem Priulanus hortus magnificus, plantis variis & raris e Syria etiam accersitis admirationi est. Omnes vero omnium, ni fallor, hortorum magnificentia simul, & stirpium in eo variarum omnis generis, e Creta etiam & aliunde peregrinarum, numero laudes facile vincit publicus ille Patavii in medicorum gratiam inclyti Senatus Veneti liberalitate institutus hortus, cui hoc tempore Aloisius Anguillara Romanus, vir in stirpium historia nostro seculo exercitatissimus atque peritissimus omnium, magna cum laude praeest."

According to Saccardo,³ Luigi Squalermo (detto Anguillara) was the first prefect "dell'orto padovano ed ostensori dei semplici" from 1546 to 1561.

From this time onwards, no doubt, the tendency was to grow as many plants as possible, and a healthy rivalry commenced between the various botanical establishments as to who could show the greatest number of different species in cultivation.

¹ Ray, J. *Travels through the Low Countries* 1: p. 182. 1738. [2nd ed.] Ray mentions the following eminent men at Padua: Aloysius Mundella, Aloysius Anguillara, Melchior Guilandinus, Jacobus Antonius Cortusus, Prosper Alpinus, Joannes Veslingius.

Saccardo, *loc. cit.* p. 7, gives the following list of Prefects of the Paduan Garden:

- 1546-1561 Luigi Squalermo (detto Anguillara).
- 1561-1589 Melchior Guilandino.
- 1590-1603 Giacom' Antonio Cortuso.
- 1603-1616 Prospero Alpini (o Alpino).
- 1616-1631 Giovanni Prevotio (Prevot).
- 1631 Giovanni Rhodio, iusto rinunciatario.
- 1631-1637 Alpino Alpini.
- 1638-1649 Giovanni Veslingio.

² Gesner, C. *De Hortis Italiae. Loc. cit.* p. 239 verso.

³ *Loc. cit.* p. 7.

In the botanic garden at Paris, for example, in the year 1636, there were about 1,800 species under cultivation and the number had risen in 1640 to 2,360, and in 1665 to as many as 4,000 species.

With the interest aroused in the collection and cultivation of plants came also the interest in their description and illustration, and many bulky and costly works were produced to illustrate the plants grown in botanic gardens.

In Great Britain the foundation of the botanic gardens at Oxford, Chelsea, and Edinburgh, was preceded by the establishment of several interesting private gardens devoted to the cultivation of medicinal herbs and plants of botanical interest, catalogues of which were published. The Rev. William Turner (1510-1568), who has been called the "Father of English Botany," had a garden somewhere at Kew and afterwards a renowned garden at Wells, when he was Dean of the Cathedral. Then there was the noted physic garden of John Gerard (1545-1612) in Holborn, at that time the most fashionable district in London, the catalogue of which—published in 1596—enumerates 1,030 plants and is of interest as being the first complete catalogue ever published of the contents of a single garden. His 'Herball,' published in 1597, was not his own work, but was simply a translation by a certain Dr. Priest of the 'Stirpium Historiae Pemptades' of Dodoens, which Gerard adopted and published as his own. On the title page of the edition of 1597, a garden is figured which has been generally considered to represent Gerard's own garden in Holborn, but as Sir Frank Crisp¹ points out, he obviously borrowed his illustration from an engraving by A. Collaert, representing a garden of A. D. 1590, in April, much in the same unscrupulous manner as he borrowed his text.

Among other early private physic gardens of interest in connection with the history of such institutions in England may be mentioned the garden of Thomas Johnson, M.D., the apothecary who had a garden on Snow Hill, in 1633—he it

¹ Guide for the use of visitors to Friar Park, Henley-on-Thames, Pt. II. Illustrations of some mediaeval gardens p. 87. 1914.

The illustration reproduced by Gerard is to be found on the title page of Tabernaemontanus, J. T. Kreuterbuch. [eds. of 1664 and 1687.]

was who brought out the improved and enlarged edition of Gerard's 'Herball' in 1638. The garden of John Parkinson (1567-1650), apothecary to James I, and King's Herbalist in Long Acre, and that of John Tradescant (died 1638) the elder, at Lambeth, are also worthy of particular mention.

John Tradescant, his father and his son were all of them botanists, collectors, and travellers. Tradescant the elder, who was gardener to various noblemen and also to Queen Elizabeth, was appointed Gardener to Charles I and founded a garden at Lambeth. This garden, after that of Gerard, was probably the most important early botanic or physic garden in England, and a catalogue of the plants therein was published in the 'Museum Tradescantianum' by his son in 1656. In addition to the garden, the Museum is worthy of notice in passing, since the curiosities it contained were bequeathed by the younger Tradescant to Mr. Ashmole, and formed the nucleus of the collection in the Ashmolean Museum at Oxford.¹

Parkinson was created King's Herbarist, "Botanicus regius primarius," by Charles I. He was a horticulturist rather than a pure botanist, and his well-known book on garden plants, 'Paradisi in sole Paradisus Terrestris,' published in 1629, probably did much to stimulate interest in the cultivation of new and rare ornamental plants. Parkinson it was who had the boldness to depict the Garden of Eden on the title page of his 'Paradisus,' and includes among other remarkable products, the "Vegetable Lamb," a pineapple, and an opuntia, the two latter plants being, as far as we are aware, unknown in the Eastern Hemisphere before the discovery of America.

Reference need only be made in passing to garden illustrations from 1580 and onwards, and to such works as the 'Hortus Floridus' of Crispian de Passe, published in Holland in 1614, and to the numerous herbals that were being produced to show the great strides that had been made in horticulture and botany in Elizabethan and early Stuart times.

The establishment of a botanic garden in Oxford in the year 1621, the nineteenth year of the reign of James I, is an

¹ See Johnson, G. W. History of English gardening p. 98. London, 1829.

important landmark in the history of botanical progress in England and follows the lead already given by the founding of university botanic gardens on the Continent.

Like them, it was "primarily founded for a Nursery of Simples, and that a professor of Botanicēy should read there and shew the use and virtue of them to his auditors."

The founding of the Oxford Garden¹ was due to the munificence of Henry, Lord Danvers, Earl of Danby, who acquired the lease of five acres of meadow land by the River Cherwell, near Magdalen College, and arranged that the University should lease the ground from the College, to whom it belonged. The land was considerably raised to prevent flooding, at great expense, and was surrounded by a wall which was completed about 1632.

Access to the Garden was by means of the Danby gateway, the foundation stone of which was laid with all fitting ceremony on St. James' Day, 1621, by the Vice-Chancellor of the University.² The following is taken from Vines and Druce:³

"Botanic Lectures.

"The next Lecture that must be mentioned is that of Botanicēy: but before I speak anything of its institution and settlement, I think it convenient that somewhat should be said of the Physic Garden, because 'twas primarily founded for a Nursery of Simples, and that a Professor of Botanicēy should read there, and shew the use and virtue of them to his Auditors.

"Henry Lord Danvers therefore, Baron of Dauntsey in the County of Wilts and Earl of Danby in Yorkshire, sometime a Gent. Com. of Christ Church, being minded to become a Benefactor to the University, thought that his money could not be better laid out than to begin and finish a place whereby learning, especially the Faculty of Medicine, might be improved. At length selecting a place without the East Gate of Oxford, near the river Cherwell, which was then meadow ground, and

¹ Daubeney, C. The Oxford Botanic Garden, popular guide. Oxford, 1850; Günther, R. T. Oxford Gardens. Oxford, 1912; Vines, S. H., and Druce, G. C. An account of the Morisonian Herbarium, etc. [Introduction.] Oxford, 1914.

² The date of the founding of the Garden has usually been incorrectly given as 1632, the year of the completion of the gateway, and in the account given by Wood of the foundation of the Garden there is a mistake of 1622 for 1621, but in their interesting epitome of the history of the garden, Vines and Druce show clearly that 1621 is the correct date when the ground was handed over and delegates were appointed.

³ *Loc. cit.* pp. IX-X.

had in ancient times been a Cemetery for the Jews of Oxon, gave to the University £250 to make a purchase of it. Upon the receipt of it they bought out the present possessor thereof, Mar. 27, 19 Jac. Dom. 1622; and not long after the University took a lease of the said ground from Magdalen College (for to them it did belong) in their own name July 28 following, by paying yearly for it 40s. Afterward much soil being conveyed thither for the raising of the ground to prevent the overflowing of the waters, the first stone of the fabric was laid on the day of St. James the Apostle (July 25) an. 1622, after this manner: About two of the clock in the afternoon, the Vicechancellor with certain Heads, Doctors, and both the Proctors, went solemnly from St. Mary's Church to that place; where being settled, Mr. Edward Dawson, a Physician of Broadgates, spoke an elegant Oration; which being done, Dr. Clayton, the King's Professor of Medicine, spake another. Afterward the Vicechancellor laid the first stone with the offering of money thereon, according to the ancient custom; then several Doctors and both the Proctors; which being done, the Vicechancellor concluded with a brief Oration.

"Afterward the said Earl proceeding in building and encompassing it with a stately free-stone wall; which being almost finished, set up in front thereof, next to the East Bridge, a comely Gatehouse of polisht stone; on which for the perpetuation of his name, he caused this Inscription to be engraven on the out and inside thereof:

GLORIAE DEI OPT. MAX.

HONORI CAROLI REGIS

IN USUM ACAD. et REIPUB.

HENRICUS COMES DANBY D. D. MDCXXXII.

In the year 1633 all the wall being finisht, and soon after the floor raised, which cost the Earl £5,000 and more, he caused to be planted therein divers simples for the advancement of the Faculty of Medicine. All which and several hundred more may now compare with any in the kingdom or elsewhere."

An interesting plan of the Garden by Loggan, made in 1675, shows four main enclosures within the boundary wall, each containing four series of geometrically arranged beds according to the formal arrangements then in vogue.

Thomas Baskerville¹ gives the following description of the early condition of the Garden (about 1670-1700):

"Amongst ye severall famous structures & curiosities where-
with ye flourishing University of Oxford is enriched, that of ye
Publick Physick Garden deserves not ye last place, being a

¹ Account of Oxford Collectanea (c. 1670-1700).

matter of great use & ornament, prouving serviceable not only to all Physitians, Apothecaryes, and those who are more immediately concerned in the practice of Physick, but to persons of all qualities seruing to help ye diseased and for ye delight & pleasure of those of perfect health, containing therein 3,000 seuerall sorts of plants for ye honor of our nation and Univer-sitie and service of ye Commonwealth."

A further interesting piece of information given by Baskerville is as follows:

"Anno 1670. Here was built by the Income of the money given by the ffounder a fair greenhouse or Conservatory to preserve tender plants and trees from the Injury of hard winter."

This conservatory covered with a roof of stone slates is shown in Loggan's plan and was of sufficient solidity to be transformed early in the eighteenth century into the herbarium, library, and professorial residence, but it was subsequently demolished.

The conservatory was heated in severe weather by means of a four-wheeled fire-basket, or wagon filled with burning charcoal, which was drawn backwards and forwards along the path by a gardener.¹

Similar conservatories, or orangeries, were common in English gardens, and the building now used as a Museum (No. III) at Kew, was erected as an orangery in 1760.

The first wooden greenhouses ever made were those erected at Oxford, in 1734, on either side of the Danby Gate.²

Although the Garden was founded in 1621, it appears that some twenty years elapsed before Jacob Bobart was appointed the first gardener, owing probably to delays caused in preparing the site. Under his supervision the Garden attained a considerable reputation and was visited by many distinguished people, including Evelyn and Pepys. Bobart's catalogue of the plants cultivated, published in 1648, enumerates 1,600 plants, 600 of which were British, and many Canadian; it may be taken as evidence of his successful management of the Garden.

¹ See *Gardeners' Chronicle* N. S. **23**: 732. f. 163. 1885. The figure is reproduced in Günther, R. T. *Oxford Gardens* p. 92. Oxford and London, 1912.

² See engraving in *Oxford Almanac*, 1766; reproduced in Günther, *loc. cit.*, plate facing p. 153.

Owing to the outbreak of the Civil Wars and the death of the Earl of Danby, in 1644, his intention to provide the University with a Professor of Botany as well as with a physic garden and a gardener, was long delayed, and the first professor, in the person of Dr. Robert Morison, was not elected to fill the office until December 16, 1669. Morison's first lecture was given in the Medicine School on September 2, 1670, and on September 5, he "translated himself to the Physic Garden where he read in the middle of it (with a Table before him) on herbs and plants for five weeks space, not without a considerable Auditory."¹

Space does not permit us to follow the fortunes of the Oxford Garden or to make mention of the many distinguished professors associated with it since its foundation, but it is of interest to remember that Sir Joseph Banks was a student at Christchurch, from 1760 to 1763, in the days of Sibthorp's professorship, a time when no lectures on botany were given and the subject was much neglected in the University.

Banks was so keenly interested in botany that he applied to Sibthorp for permission to procure a qualified lecturer to be paid entirely by the students. This request being acceded to and a sufficient number of students having been obtained, Banks went to Cambridge and secured the services of a Mr. Lyons, a botanist and astronomer, for the purpose.² The assistance rendered by the sister university in the botanical education of one who was to achieve such great things for the science and to have so large a share in directing the fortunes of the Royal Gardens at Kew, is worthy of more particular notice since botany was not officially recognized in Cambridge until 1724, when a professor was appointed, and there was no botanic garden there until the year 1762.

The Botanic Garden at Edinburgh, which now claims attention, has had a somewhat involved history, as the present Royal Botanic Garden is the sixth and only remaining botanic garden in the Scottish capital, though in the early years of

¹ Vines, S. H., and Druce, G. C. *loc. cit.*, p. XXIV.

² Anonymous, Sir Joseph Banks and the Royal Society p. 62. London, 1844.

the eighteenth century there were three distinct gardens in Edinburgh.

The original Edinburgh Garden was founded by Sir Robert Sibbald and Sir Andrew Balfour, physicians, for the cultivation of medicinal plants in order "to safeguard the Practitioner against the Herbalist and to enable him to have a correct knowledge of the plants which were the source of the drugs he himself would have to compound."¹

For this purpose they acquired the lease of a small area of ground near Holyrood, and James Sutherland was secured to look after it and instruct the apprentices and lieges in botany. Such success attended the venture that a piece of the Royal Flower Garden at Holyrood was assigned to the cultivation of medicinal plants and this with the title of Physic Garden became the Royal Botanic Garden in Scotland.

In 1767 the same physicians acquired from the Town Council of Edinburgh a lease of the Garden of Trinity Hospital and adjacent ground—a site now partly occupied by the Waverley Station—and Sutherland was appointed to lecture on botany as Professor in the Town's College, now the University, and to be in charge of this new Physic or Town's Botanic Garden. Then in 1702 another botanic garden was established by the University—the College Garden—of which Sutherland was also placed in charge. The distance of the two existing gardens being too great from the University, Sutherland resigned the care of the Town's Garden and College Garden in 1706, but remained King's Botanist, retaining the Keepership of the Royal Botanic Garden, and the Town Council appointed a professor to take charge of the Town and College Gardens. There were thus two rival botanical schools with their gardens in Edinburgh, and it was not until the year 1739 that the rivalry was terminated by the appointment of Dr. Charles Alston, the then Keeper of the Royal Botanic Garden, to the University Chair—a combination which holds to the present day by consent of the Crown and the University.

¹ Balfour, I. Bailey. *History of the Royal Botanic Garden, Edinburgh*. Notes of the Roy. Bot. Gard., Edinburgh 4: 1904. Historic Notice. pp. v-viii.

Between the years 1760 and 1786 a new site was found for a botanic garden and the other gardens were abandoned. This new garden, formed during John Hope's keepership, eventually became unsuitable owing to the growth of the town, and the present site (twenty-seven acres) was selected about 1820, during the keepership of Professor Graham.

The Edinburgh Garden, through the University, still retains its connection with the Medical School, and the instruction of the medical student is one of the functions of the Professor and his staff. With its fine collections of living plants, its herbarium, library, laboratories, and remarkable series of specimens in the museums, the Edinburgh institution may well serve as an example of the ideal botanic garden.

The Chelsea Physic Garden,¹ which next claims attention, was founded as the Garden of the Society of Apothecaries² in London in the year 1673. The earlier garden of the Society had been at Westminster, but this had no river frontage, and the ground at Chelsea was leased from Charles Cheyne, in 1673, as a convenient spot for building a barge house for their processional barge in which they attended city functions, as was customary for city companies.

In 1676 the plants at Westminster were moved to the Chelsea Garden, which had already been suitably enclosed with a wall. The freehold of the Manor of Chelsea, including the Physic Garden, was purchased in 1712 by Dr. (afterwards Sir Hans) Sloane, who in the year 1722 conveyed the Garden by deed to the Society of Apothecaries. The conveyance was made "to the end that the said garden might at all times thereafter be continued as a Physick Garden, and

¹ Field, H., and Semple, R. H. *Memoirs of the Botanic Garden at Chelsea*. London, 1878.

² The Society of Apothecaries itself was formed in 1617 "that the ignorance and rashness of presumptuous Empirics and unexpert men might be restrained, whereby many discommodities, inconveniences and perils do daily arise to rude and incredulous people." See Blunt, R. *Cheyne Walk and thereabout* p. 99. London, 1914.

Certain continental botanic gardens, such as the ancient garden at Salzburg were founded in connection with local pharmaceutical schools and have had no connection with any university.

for the better encouraging and enabling the said Society to support the charge thereof, for the manifestation of the power, wisdom, and glory of God in the works of the creation, and that their Apprentices and others might better distinguish good and useful plants from those that bore resemblance to them, and yet were hurtful and other the like good purposes."¹

The utilization of the Garden for the sole purpose of growing medicinal plants to be converted into drugs for the Society's use was prohibited by Sir Hans Sloane's deed of gift, and he definitely encouraged the science of botany by making it a condition that fifty specimens of distinct plants, well dried and preserved, which grew in their garden that same year, with their names and reputed names, were to be delivered yearly to the President and Fellows of the Royal Society of London, "until the number of two thousand had been attained." He also enjoined that the plants so presented in each year were to be specifically different from those presented in every former year; and this injunction was more than faithfully carried out by the Society.²

The Garden achieved some notoriety in having been the first garden in England where the Cedar of Lebanon was planted; the final survivor of the four placed there in 1683 was only removed in the year 1904.

John Evelyn, who visited the Garden in 1685, was impressed by the heating arrangement of the greenhouses, then quite an innovation. "What was very ingenious," he remarks in his diary, "was the subterranean heate conveyed by a stove under the conservatory, which was all vaulted with bricks, so as he³ has the doores and windows open in the hardest frosts, secluding only the snow." An arrangement far more efficient and useful than the remarkable open fire-baskets formerly in use at Oxford.

¹ Perrédès, P. É. F. *London Botanic Gardens*. Wellcome Chemical Research Laboratories, London, Publ. 62: p. 57. London, 1906 (transferred from the present to the past tense).

² Johnson, G. W. *History of English gardening* p. 150. London, 1829.

³ John Watts, appointed gardener in 1680.

The appointment of Philip Miller,¹ in 1723, as Head Gardener, is an important event in the history of the Garden, both for the value of his services to the Garden itself and for his widespread influence on botany and horticulture.

At the time of Miller's appointment, exotic plants were pouring in from every clime under the patronage of a general taste for their acquisition. Hothouses were multiplying and their inhabitants accumulating to a hitherto unheard-of extent, and a man of Miller's practical skill and botanical knowledge was needed not only to demonstrate his skill, but also to impart his knowledge for the use of others. From his 'Dictionary' it can be seen that many plants were grown and flowered at Chelsea for the first time under cultivation.

William Aiton (1731-1793), the first Curator of the Royal Gardens at Kew, was a pupil under Miller at Chelsea, nor must Nathaniel Bagshaw Ward, Examiner to the Society of Apothecaries from 1836 to 1854, the inventor of Wardian cases, be forgotten. His invention made possible the introduction of the tea plant to India by Robert Fortune (Curator of the Chelsea Garden, 1846-1848), of *Cinchona* from South America to Kew by Markham, and thence to India, and of many other valuable products to botanic gardens which have subsequently been disseminated for the use of mankind. Not the least useful of the activities of the Chelsea Physic Garden were the herborizing excursions around London, under the charge of the Demonstrator of Plants, which were maintained for some two hundred years. The Physic Garden has suffered many vicissitudes in the course of its existence, and towards the end of the last century almost ceased to exist, but fortunately a new arrangement for its maintenance was made in 1899.² Reorganized under the new scheme and with its modern greenhouses and laboratory, the Chelsea Garden has entered on a sphere of usefulness in connection with the teaching of botany and the provision of material and opportunity

¹ Charles Miller, son of Philip (who had aided in the selection of the site), was made first Curator of the original Cambridge University Botanical Garden founded in 1762.

² The Chelsea Physic Garden. First Report of Committee of Management, 1905, with plan of the Garden in 1753.

for botanical investigation as great if not greater than at any time in the past.

The origin of the Royal Botanic Gardens, Kew, was due to the interest in botany displayed by Princess Augusta, Princess Dowager of Wales, under the guidance of Lord Bute, an enthusiastic botanist; and a piece of the Royal Garden attached to Kew House was set apart in 1760 for the purpose of forming a physic garden.

"The space allotted consisted originally of nine acres, enclosed by walls (the ornamental building now standing, called the Temple of the Sun, being then nearly the centre of the Garden), which was laid out and scientifically planted in two divisions, one containing a collection of herbaceous plants, arranged according to the Linnean system, then in its infancy, but with which Aiton had become well acquainted while serving under Miller. This division was called the Physic Garden.

"The second division was called the Arboretum, containing all the then known introduced hardy trees and shrubs scientifically arranged. Within the area were several Glass houses, and in 1761 a large hothouse, 110 feet long, was erected by Sir Wm. Chambers . . . in after years known as the Great Stove. In the same year an Orangery, 130 feet long, was also erected."¹

No doubt several of the old and interesting trees now standing near the Temple of the Sun were planted in Princess Augusta's arboretum soon after the foundation of the Garden.

William Aiton was placed in charge of the Garden under the direction of Lord Bute, and was Chief Gardener from 1759 to 1793. Sir W. Chambers, the designer of the Pagoda and most of the Temples still to be seen in Kew, gives the following account of Princess Augusta's Physic Garden:

"The Physic or exotic garden was not begun before the year 1760; so that it cannot possibly be yet in perfection: but from the great botanical learning of him who is the principal man-

¹ Smith, John. Records of the Royal Botanic Gardens, Kew. p. V. 1880. See also Kew Bull. Misc. Inf. 1891: 289-294. 1891.

The Great Stove stood near the Temple of the Sun and was removed in 1861. Its site is marked by an old wistaria, trained on an iron cage which grew upon its walls. The method of ventilating the house was designed by William Hales, the physiologist, who described his method in a letter to Linnaeus written in 1758. The method is in use at Kew to-day and was devised independently by Sir W. T. Thiselton-Dyer.

The Orangery is now Museum No. III.

ager and the assiduity with which all curious productions are collected from every part of the globe without any regard to expense, it may be concluded that in a few years this will be the amplest and best collection of curious plants in Europe.”¹

With the death of Princess Augusta in 1772, George III inherited the Kew property and united the gardens of Kew House with those lying contiguously, which formed the gardens of the Palace of Richmond, and so produced the extensive domain now occupied by the Royal Botanic Gardens. To the great benefit of Kew, George III chose Sir Joseph Banks as his botanical adviser, and for forty-eight years Sir Joseph directed the affairs of the Gardens. During his term of office the practice of sending out collectors was established, a practice fraught with discoveries of wide-spread interest and value for horticulture and botany. Of the many Kew collectors² it is well to mention in particular the following: Francis Masson, the famous collector of Cape plants; David Nelson, assistant botanist on Cook’s third voyage, who subsequently died from exposure after the mutiny of the *Bounty*; Archibald Menzies, who travelled in Australia and Chili and introduced *Araucaria imbricata*; William Ker, the collector in China, who in 1812 became Superintendent of the Royal Botanic Garden, Ceylon; and Allan Cunningham, whose travels took him to Brazil, the Cape, Australia, Tasmania, New Zealand and Norfolk Island. Cunningham returned to Australia, in 1836, to fill the post of Superintendent of the Botanic Garden at Sydney.

The days of Sir Joseph Banks were indeed the Golden Age of Kew, and under his direction the Royal Gardens became a center of botanical exploration and horticultural experiment unparalleled before or since. The well-known lines of Erasmus Darwin³ refer to the Kew of Sir Joseph Banks’ day, enriched by the labors of her collectors:

¹ Chambers, Sir W. Plans, elevations, sections and perspective views of the gardens and buildings at Kew in Surrey, the seat of Her Royal Highness, the Princess Dowager of Wales p. 3. Brentford, 1765?

² For the complete list of Kew collectors, see Kew Bull. Misc. Inf. 1891: 295–311. 1891.

³ The Botanic Garden. 1791.

"So sits enthroned, in vegetable pride,
 Imperial Kew by 'Thames' glittering side;
 Obedient sails from realms unfurrow'd bring
 For her the unnam'd progeny of Spring;
 Attendant Nymphs her dulcet mandates hear,
 And nurse in fostering arms the tender year;
 Plant the young bulb, inhume the living seed,
 Prop the weak stem, the erring tendril lead;
 Or fan in glass-built fanes the stranger flowers,
 With milder gales, and steep with warmer showers.
 Delighted Thames through tropic umbrage glides,
 And flowers antarctic, bending o'er his tides;
 Drinks the new tints, the sweets unknown inhales,
 And calls the sons of Science to his vales."

George III and Sir Joseph Banks both died in 1820, and for some twenty years the Royal Gardens gradually fell into a condition of sad neglect. In the early years of the reign of Queen Victoria, however, the Royal Gardens were restored to their proper position as the National Botanical Garden, thanks to the devoted labors of the committee of which John Lindley and Sir Joseph Paxton were the distinguished members, and Sir William Hooker was appointed Director of the Royal Botanic Gardens in 1841. Thence onwards, under Sir Joseph Hooker, and Sir William Thiselton-Dyer, the history of Kew has been one of steady progress and usefulness and the Royal Botanic Gardens have played a prominent part in connection with all matters of botanical enterprise in the British Colonies.¹

¹ The establishment at Kew comprises: I. The Botanic Gardens and Arboretum (288 acres); II. The Herbarium and Library; III. The Museums devoted to (i and ii) dicotyledons and monocotyledons and their economic products, (iii) exotic timbers and conifers, (iv) British forestry, and (v) The North Gallery of paintings by Miss Marianne North; IV. The Jodrell Laboratory for scientific research; V. The Pathological Laboratory; VI. Director's Office.

The more important books dealing with the history of Kew and its collections are:

1. Aiton, W. *Hortus Kewensis*, 3 vols. London, 1789.
2. Aiton, W. T. *Hortus Kewensis*, 5 vols. London, 1810-13. [2nd ed.]
3. Scheer, F. *Kew and its Gardens*. Richmond, 1840.
4. Historical account of Kew to 1841. *Kew Bull. Misc. Inf.* 1891:279-327. 1891.
5. *Royal Botanic Gardens, Kew, Reports on progress and condition*. 1855-1882.
6. Perrédès, P. É. F. *London Botanic Gardens*. Wellcome Research Laboratories, London, Publ. 62: 17-40. 1906.
7. Bean, W. J. *The Royal Botanic Gardens, Kew*. London, 1908.
8. *Popular Official Guide to the Royal Botanic Gardens*. Kew, 1912.
9. *Kew Bull. Misc. Inf.* 1887.
10. *Kew Plant Lists and Museum Guides*.
11. Smith, J. *Records of the Royal Botanic Gardens, Kew*. London, 1880.

Kew, having no connection with any university or educational establishment,¹ differs markedly in this respect from the botanic gardens to which allusion has been made. Her sphere of usefulness is largely concerned with the economic aspect of botany, and it is her aim and object to encourage and assist, as far as possible, scientific botanists, travellers, merchants and manufacturers, in their varied botanical investigations.

Space does not permit of more than a brief mention being made of the new Berlin Garden at Dahlem and of many other important gardens on the Continent and in Great Britain and Ireland. The Berlin Botanic Garden² was founded in 1679 in the heart of the city, and in 1801 it was reorganized and improved. The removal of the Garden to its present site at Dahlem was completed in 1909. The new Garden with its geographical and ecological arrangements of the plants and the splendid Botanical Institute and Museums, now forms one of the finest schools of botany in the world. In her aims and objects she compares more closely to Kew than to any other botanic garden.

The following notes refer to other important gardens not specifically mentioned in the text:

The Upsala Garden (founded 1655-57) was injured by the great fire in 1702, and remained neglected until 1741. The restoration was begun by Rosen and energetically taken up by Linné. (See Swederus, M.B. Botaniska Trädgården, Upsala, 1655-1807. Falun, 1877.) The Imperial Botanic Garden of Peter the Great, Petrograd (St. Petersburg), was founded in 1713 (see Kew Bull. Misc. Inf. 1913: 243-252. 1913), and that of Vienna in 1754.

The Cambridge Botanic Garden was founded in 1762 by Richard Walker, D.D., formerly Vice-Master of Trinity College. The Garden was transferred to its present site in 1846 and occupies about twenty acres. It is in close connection with the Botany School at Cambridge and provides abundance of material for research work and for the teaching purposes of the Botany School. The Garden is also fitted with a small laboratory. Some eighteen acres are available for extension.

¹ Lectures and demonstrations in chemistry and physics, general botany, systematic and geographical botany, economic botany, plant pathology and on soils and manures are given in the Gardens to the young gardeners at Kew.

² See Urban, I. Geschichte des Königl. botanischen Gartens und des Königl. Herbariums zu Berlin, nebst einer Darstellung des augenblicklichen Zustandes dieser Institute. Festschr. naturwiss. u. med. Staatsanst. Berlin, 1881.

Engler, A., and others. Der Kgl. bot. Garten und das Kgl. bot. Museum zu Dahlem. Berlin, 1909.

The Royal Botanic Gardens, Glasnevin, Dublin, were founded in 1790, through the influence of Dr. Walter Wade and the Hon. Dublin Society, and in 1877 were transferred to the Science and Art Department. The Botanic Garden of Trinity College, Dublin, was established in 1806-08. (See Notes from the Botanical School of Trin. Coll., Dublin 1: p. 3. 1896.)

The garden at Breslau was founded in 1811. The Geneva Garden, founded in 1817, has recently been transferred to a new site. The Munich Garden was founded in 1822 (see Martius, Hort. Bot. R. Acad. Monacensis p. 5. 1825.) It is now one of the most interesting gardens on the Continent and forms an integral part of the new and magnificently equipped Botanical Institute.

The Glasgow Botanic Garden was established in 1817, having been preceded by an earlier Physic Garden; in 1841 the garden was moved to its present site and now occupies about forty acres (see Sherry, C. The Glasgow Botanic Gardens. Glasgow, 1901).

The botanic gardens whose history has been sketched in the preceding pages can all trace back their origin to the herb gardens of mediaeval times and the physic gardens of the early universities. Their *raison d'être*, the growing of simples for the medical profession, has resulted in the exploration of the globe for the useful, the beautiful, and the curious in the vegetable kingdom. A few other botanic gardens, however, remain to be considered, whose origin must be traced to a different motive. These gardens lie within the tropics, and the desire to participate in the valuable trade in spices, then a monopoly of the Dutch, led to the establishment of gardens for the cultivation of various spices and other important economic plants during the latter part of the eighteenth century.

The credit of establishing economic gardens in the tropics belongs to Great Britain, and the experiment, started with the founding of the botanic garden in the Island of St. Vincent, in 1764, has been continued, at times somewhat intermittently, until at the present day a botanic garden or station is to be found in almost every British dependency and possession.

The lead given by Great Britain has been followed by other nations and several notable achievements have resulted. Foremost among these must be mentioned the Botanic Gardens at Buitenzorg, Java,¹ probably the most complete and exten-

¹ The complete institution at Buitenzorg, known as "Lands Plantentium," is divided into nine Departments: I. Herbarium and Museum; II. Botanical

sive botanical establishment in the world. The garden was founded in 1817 at the suggestion of Reinwardt,¹ and Dr. C. L. Blume was appointed the first Director when Reinwardt left Java to become Professor at Leiden. The first Curator, James Hooper, had been trained at the Royal Gardens, Kew. The valuable scientific researches in pure and applied botany carried out at Buitenzorg are too well known to require detailed description, and allusion need only be made to the important encouragement given to the cultivation of *Cinchona*, rubber, coffee, and other economic products in Java, through the medium of the Botanic Gardens.

The earliest tropical botanic garden appears to have been that founded in the West Indies at St. Vincent, in 1764.² A garden of about forty acres was established with Government House in the center, as a place where plants "useful in medicine and profitable as articles of commerce might be propagated and where nurseries of the valuable productions of Asia and other distant parts might be formed for the benefit of His Majesty's Colonies." Plants intended for the West Indies were lost owing to the mutiny of the Bounty in 1790, but three years later Captain Bligh succeeded in landing a valuable consignment of plants from the Pacific, including the bread fruit, and a few years after, nutmegs, cloves, and other spice plants were introduced.

Until 1815 the Garden flourished, when interest was shifted to Trinidad, where a garden was formed in 1817, and many

Laboratories; III. Agricultural and Experimental Garden (151 acres) with laboratory for agricultural chemistry; IV. Pharmacological Laboratory; V. Botanic Garden (145 acres), Mountain Garden (77 acres and 700 acres virgin forest), and Laboratory; VI. Office, Library, and Photographic Laboratory; VII. Forest Flora collections; VIII. Laboratory for the study of Deli tobacco; IX. Coffee Experiment Station (the two last are partly private institutions).

¹ It is possible that the original idea of founding a botanic garden at Buitenzorg was made by Sir Stamford Raffles, when Governor of Java, during the few years (1811-17) that Java was a British possession. Near the entrance there is a small monument to the memory of Lady Raffles, who died in Java during the British occupation of the island.

² Guilding, Rev. Lansdown. An account of the botanical garden in the island of St. Vincent. Glasgow, 1825. See also Kew Bull. Misc. Inf. 1892: 92-104. 1892.

of the plants were removed thence from St. Vincent. The St. Vincent Garden was restored in 1890 and now, fortunately, there is a botanic garden or station in every West Indian island of importance. These serve as centers for the distribution of economic plants and of scientific information, and have also become gardens of peculiar charm for the refreshment and recreation of the inhabitants.

The gardens of the East, however, are preëminent among tropical botanic gardens owing to the vastness of the territory over which they exercise their influence. Foremost among these, after Buitenzorg, is the Calcutta Botanic Garden, founded in 1786 on the suggestion of Lieut. Col. Robert Kyd.

This garden was intended to be the source of botanical information for the possessions of the East India Company, and also the center to which exotic plants of economic interest could be imported for experimental cultivation and thence distributed.¹

It was hoped at first that the spices which rendered the trade of the East India Company with the Moluccas, etc., so lucrative, might be cultivated in Bengal, and Kyd's earliest efforts were directed to the introduction of cloves, nutmegs, cinnamon, and pepper vines, but the climate of northern India proved unsuitable. Much was attempted and, despite numerous failures, much accomplished in the way of new introductions in the early days, the failures possibly being as important as successes since it was soon evident what could or could not be grown in Bengal. The Calcutta Gardens, however, despite the failure in their original intention, have under their distinguished superintendents achieved notable results. The introduction of tea to India—one of Kyd's original ideas—was mainly carried out through the instrumentality of the Gardens, and potato growing, the introduction of mahogany, jute, sugar-cane, and the improvement of Indian cotton cultivation, may be counted among its many benefits to the people of India.

¹ King, George. Guide to the Royal Botanic Garden, Calcutta. 1895.

But most important of all was the part played by the Garden in the introduction of *Cinchona*¹ from South America to India with the coöperation of Kew, and the subsequent cultivation of Peruvian bark in the Sikkim Himalaya. The Calcutta Garden in this particular has retained the ancient connection of botanic gardens with medicine perhaps more than any other similar institution. The cultivation of the quinine-yielding cinchonas has been carried to such a successful issue in the plantation and factory at Sikkim under the superintendents of the Garden, notably Sir George King, that government hospitals and dispensaries have for years been supplied from this source with all the quinine required for them; while 5-grain doses of the same drug can be purchased for a pice each (equal to about $\frac{1}{4}$ d. English) at every post-office in the Province.²

Associated with the Garden are the valuable herbarium and the economic museums, the whole forming an institution capable of responding fully to the botanical requirements of the Indian Empire.

The history of botanic gardens would be incomplete without reference being made to the foundation of such institutions in Malaya and Ceylon. At Penang³ the Hon. East India Company decided to start spice gardens with a view of breaking down the Dutch monopoly. Living plants of nutmegs and cloves were collected in the Moluccas in 1796, and the first nutmegs were produced in Penang in 1801.

The Gardens, however, were destroyed⁴ in 1805, and re-founded in 1822 at the instance of Sir Stamford Raffles. He it was who founded the Singapore Gardens in 1823, and intro-

¹ See Markham, Sir C. R. *Peruvian Bark*. London, 1880.

² *Guide to Royal Botanic Garden, Calcutta* p. 6. 1902. [Revised ed.]

³ Ridley, H. N. *The abolition of the Botanic Gardens of Penang*. Agr. Bull. Straits and Fed. Malay States 9: p. 97. 1910.

⁴ *Ibid.* p. 104.

	founded	abolished
First Penang garden	1800	1805
Second Penang garden	1822	1826
Third Penang garden	1884	1910
First Singapore garden	1823	1829
Second Singapore garden	1878 and still existing.	

duced nutmegs, cloves, and cacao, but the Garden was unfortunately abolished in 1829.

The botanical enterprise of this remarkable man in Java, Malaya, and Sumatra, deserves an honorable place in our botanical history, and no more fitting memorial of his genius could be found than the present beautiful garden at Singapore, founded in 1878, which has so ably upheld the best traditions of the founder of the original garden.

The first botanic garden established in Ceylon¹ was created by the Dutch on Slave Island, near Colombo, but this was neglected when the island passed into the possession of Britain, and it was not until 1810, when Sir Joseph Banks suggested a site, that a new garden was established, also on Slave Island at a place still known as Kew. William Ker was transferred from Canton, in 1812, and appointed superintendent. The Garden was not a success, owing to its situation, and in 1821, during the superintendence of Alexander Moon—who had been sent out by Banks—the Garden was transferred to Peradeniya. In its new site its history has been a record of prosperity, and its usefulness has been considerably increased by the formation of additional gardens in different parts of the island suitable to the varied climatic conditions of the country.

The scientific researches in pure and applied botany, in tropical mycology and chemistry, and the cultural experiments which have been carried out in the Gardens and laboratory in Ceylon have thoroughly justified the existence of the institution at Peradeniya, and prove, if proof were needed, the inestimable value of scientific botanical establishments in the tropics.

The colonizing of Australia soon led to the foundation of botanic gardens, and those at Sydney² have the honor of being the first to be founded in the Australian Continent.

¹ Trimen, Henry. *Hand guide to the Royal Botanic Gardens, Peradeniya.* Colombo, 1885.

² Sydney Botanic Gardens. *Kew Bull. Misc. Inf.* 1906: 205–218. 1906.

Maiden, J. H. Presidential address to the Royal Society of New South Wales, 1912. *Roy. Soc. N. S. Wales, Jour. and Proc.* 46: 1–73. 1912. [See p. 49.]

These Gardens occupy the site of the Government Garden established in 1788, and here the first exotic plants were installed in the same year. Owing to the great demand for New Holland plants, due largely to the interest taken in them by Sir Joseph Banks, a vigorous exchange in plants soon grew up between the Sydney Gardens and the outside world, to the great profit of the institution, which appears to have been definitely founded as a botanic garden in the year 1816.

Sydney is now fully equipped for botanical work with its renowned Botanic Gardens, its university department of botany, and museum.

Other well-furnished botanic gardens are to be found at Brisbane, Melbourne, Adelaide, Hobart, and Tasmania; at Melbourne and Adelaide their value is enhanced by association with the botanical departments of the universities.

Flourishing botanic gardens are also established in New Zealand, at Wellington, Dunedin, Napier and Christchurch.¹

Before leaving the subject of botanic gardens in British Dominions, mention must be made of the foundation only last year (1913) of the National Botanic Garden of South Africa, at Kirstenbosch,² which, though the most recent of such gardens, bids fair to take a place in the front rank of the botanic gardens of the world, both on account of the admirable nature of the site and the remarkable character of the South African flora. The predecessor of this garden was the Cape Town Botanic Garden, founded in 1848, which became the Municipal Garden of Cape Town in 1892, after a somewhat chequered career.³

The Municipal Gardens at Durban, Natal, established in 1853 as the Natal Botanic Garden, have played an important part in botanical enterprise in South Africa and at no time more than under the directorship of Dr. J. Medley Wood. It

¹ The Botanic Gardens at Hong Kong with their herbarium form a valuable center for Asiatic botany, nor must the Gardens at Tokyo and other important Japanese centers of botanical activity be omitted. Botanic gardens have been established also in Fiji, Seychelles, Mauritius, etc.

² Kew Bull. Misc. Inf. 1913: pp. 309-314, and p. 373. 1913; Nature 93: 190-191. 1914.

³ Kew Bull. Misc. Inf. 1892: 10-14. 1892.

would be a most unfortunate occurrence should the activities of this important garden, small though it is, be in any way curtailed or its functions abrogated by the change in its administration or owing to the establishment of the new National Garden.¹

In America,² botanic gardens have been in existence since the year 1728, when John Bartram founded a botanical garden in Philadelphia. Though no longer a botanic garden, the plot of ground still remains and serves as an interesting landmark in the history of North American botany.³ The foundation of the Elgin Botanic Garden by Dr. David Hosack, in 1801, was an important advance and the Garden of some twenty acres was gradually stocked with a large and valuable collection of plants.⁴ In 1810 it became the Botanic Garden of the State of New York and was subsequently granted to Columbia College. It has ceased to exist as a garden, but it will be always held in remembrance from its association with the work of its founder, of Amos Eaton, John Torrey, and Asa Gray.

The founding of the New York Botanical Garden, as a result of the untiring energy of Dr. N. L. Britton and the Torrey Botanical Club, may be regarded as a worthy monument to the memory of these pioneers in American botany. Furnished as it is with the Torrey Herbarium, the value of which has been enhanced by vast acquisitions—including the Chapman and Meisner herbaria—the library, museum, and laboratories, the New York Botanical Garden, in association with the Department of Botany of Columbia University, rivals

¹ Other botanic gardens and stations in Africa have been established in Uganda, in the British and French West African Colonies and at Victoria in the German Cameroons. In Algeria there is the fine old "Jardin d'essai" at Algiers.

² In Canada there is a botanic garden at Ottawa in connection with the Agricultural Department, and a small garden at Montreal belonging to the botanical department of McGill University.

³ Bartram, through Peter Collinson, appears to have received seeds from Philip Miller of the Chelsea Physic Garden. See Wilbert, M. I. Some early botanical and herb gardens. *Am. Jour. Phar.* 80: 412-427. 1908. [See p. 416.]

⁴ Hosack, David. A statement of facts relative to the establishment and progress of the Elgin Botanic Garden, etc. New York, 1811.

Wilbert, M. I. *Loc. cit.* p. 423.

in its completeness, if it does not already excel, any botanical institution in the Old World.¹

The Botanic Garden of Harvard University, which was founded in 1805, next claims attention. The garden itself is small, but in combination with the herbarium containing Gray's collection, the museums, library, and laboratories, it forms a botanical institution singularly complete and efficient.

With the Arnold Arboretum situated close at hand, Harvard has become a Mecca for botanists all the world over. The Arboretum,² founded by Mr. James Arnold, covers at present about two hundred and twenty acres, and the collection of trees and shrubs brought together by the remarkable industry of Professor Sargent is unrivalled, and it stands to-day for one of the most interesting and valuable developments of the principles of a botanic garden. To Professor Sargent, as well as to such enlightened men as the de Vilmorins and the firm of Veitch, the gardening world also owes a great debt of gratitude for the introduction of countless new hardy plants for the enrichment of our gardens.

Important work is being performed by the United States Department of Agriculture, at Washington, in the introduction of new plants, nor should the part played by the herbarium of the United States National Museum be forgotten in this connection. Allusion may also be made at this point to the Desert Laboratory at Tucson, and to the importance of the experimental work which is being undertaken in Hawaii, Cuba, and the Philippine Islands.

Other botanic gardens are those of the Michigan Agricultural College (1877), the University Botanic Garden at Berkeley, California, the Botanic Garden of the University of Pennsylvania at Philadelphia, of Smith College at Northampton, and the Buffalo Botanical Garden. These each and all are of recent foundation and have been established in response

¹ Britton, N. L. Botanical Gardens. N. Y. Bot. Gard., Bull. 1: 62-77. 1897; Underwood, L. M. The department of botany and its relation to the New York Botanical Garden. Columbia Univ. Quart. 4: 278-292. 1903; Britton, N. L. Botanical Gardens. Bull. Torr. Bot. Club 23: 331-345. 1896. [See pp. 341-345.] See also Britton, N. L. *Loc. cit.* pp. 72-77.

² Kew Bull. Misc. Inf. 1910: 261-269. 1910.

to the need of such institutions for teaching and research in botany.

Finally there is the Missouri Botanical Garden,¹ founded in 1889 by the munificence of Henry Shaw, in pious memory of whom this Twenty-fifth Anniversary Celebration is being held.

Founded on broad lines and generously endowed, the Garden has already established itself as one of the important botanic gardens of the world. With its herbarium, library, and laboratories, and the close relationship with the Shaw School of Botany of Washington University, the future of the Missouri Botanical Garden cannot fail to be one of ever-increasing usefulness.

It is a matter of regret to all botanists that South America, so rich a storehouse of botanical treasures, should contain so few important botanic gardens. The magnificent Garden at Rio de Janeiro,² founded in 1808, the Botanic Gardens at Santiago in Chili,³ at Georgetown, British Guiana, and at Buenos Aires represent the measure of botanical enterprise in the continent.

The botanical possibilities at Rio de Janeiro are very great, and the Garden, in addition to its collection of living plants, possesses the herbarium of Martius, a library and laboratories. When the interest in botanical science becomes fully aroused in Brazil, a striking development of the botanic garden may be confidently expected.

¹ Trelease, W. The Missouri Botanical Garden. First annual report of the Director, for 1889. *Mo. Bot. Gard., Rept.* 1: p. 91. 1890.

Trelease, W. The Missouri Botanical Garden. *Pop. Sci. Month.* 62: 193-221. 1903.

² Rodrigues, J. B. *Hortus Fluminensis*. Rio de Janeiro, 1894.

³ Philippi, F. *Vorgeschichte des botanischen Gartens von Santiago*. *Gartenflora* 31: 6-9. 1882. The date of the foundation of this garden is uncertain. herbarium and museum attached to the University. See also Philippi, F. It contains a very interesting collection of plants and trees, and there is a good *Memoria i catalogo de las plantas cultivadas en el Jardin Botanico*. Santiago de Chile, 1884.

FUNCTIONS OF BOTANIC GARDENS

The varied functions performed by botanic gardens in the course of their history have been indicated to some extent in the preceding pages, and the gradual change in function from that of the purely medicinal garden for the growing of simples to the fuller conception of the true botanic garden has been traced.

With the increase in knowledge and interest in botany, new plants were brought into cultivation from all sources and gardens threatened to be overwhelmed by unarranged masses of material. Classification, therefore, became a necessity and various systems began to be put forward in response to the demand. To these we cannot do more than make brief allusion. After the efforts of Caesalpino came Morison's system of classification, which did not receive general acceptance and was absorbed into that of Ray, and neither system found many adherents as regards the disposition of plants in the botanic gardens.

The two early systems which really dominated plant arrangement were those of Linnaeus and Jussieu, the latter finding acceptance in France, where the Linnaean system never became established.

To France, in consequence, we must look for the evolution of the natural system of classification, and, with its adoption, botanic gardens gradually developed into a means of providing a synoptical illustration of the whole vegetable kingdom.

It was in the Trianon gardens that Bernard and A. L. de Jussieu, towards the close of the eighteenth century, evolved the idea of grouping plants according to a system based on natural affinities, and the Trianon system was quickly imitated and elaborated in course of time by Gärtner, De Candolle, Robert Brown, and others.

With the revival of interest in plant collecting a new development took place, and plant geography came to the front as a basis of plant arrangement in botanic gardens. Thus collections were made to represent the floras of definite regions, such as that of New Holland or The Cape, and af-

forded instructive and useful aids to the study of botany and plant distribution in particular.

These two tendencies in botanic garden arrangement hold good at the present day, and gardens may be found adhering to one or the other plan. Both systems have their merits, and where possible both may be followed with due regard to local conditions, but a slavish adherence to the one or to the other tends to court disaster and produce confusion rather than edification.

There is much to be said for the older ideas of separating "herbaceous plants" from "trees and shrubs," and for making an independent arrangement of the two classes, mainly on the ground of cultural requirements.

The natural system in plant houses, again, is almost certainly doomed to failure, and an arrangement on geographical or ecological lines must perforce be adopted.

How instructive such an arrangement may be is shown by an arrangement of plants from alpine regions or by a collection of xerophytes representative of some particular desert area of the globe.

Plant physiology affords another basis for plant arrangement and perhaps is fruitful of greater educational value than almost any other system. It has the further advantage that it lends itself to adoption in the smaller garden where a complete conspectus of the vegetable kingdom is an impossibility.

In some botanic gardens on the Continent, particularly at Berlin, and to a smaller extent at Geneva and elsewhere, the flora of mountain regions is arranged with an attempt at actual verisimilitude as to soil conditions and altitudinal distribution of the zones of vegetation. The idea is an excellent one, but its realization is liable to be far from perfect since the limiting factors of altitude and climate are absent and the plants of the mountain tops, deprived of their natural restrictions, tend to usurp more than their proper share of available space.

In whatever manner the main garden may be arranged, there should always be special portions set apart for certain well-marked plant types, such as alpine and rock plants, suc-

culents, bulbous plants, halophytes, bog and water plants, and the like, and if possible there should also be a definite economic and medicinal garden. Plant houses should also be set apart for economic plants where such as are of definite medical and economic values may be studied in connection with their products displayed in the museums.

The exact determination of plants of economic value, especially in connection with the vegetation of the tropics, is a matter of such importance that the necessity of a well-furnished herbarium and museum, in connection with a botanic garden of any pretension, needs no demonstration. With the aid of the herbarium, also the correct determination of all plants cultivated in a botanic garden should be ensured.

Just as necessary for the complete botanical establishment is the possession of a laboratory both for the examination and analysis of plants, and also for the study of such problems in mycology, plant physiology, plant hybridization, etc., as can be studied nowhere at greater advantage than in a botanic garden.

A somewhat unexpected exhibition in a botanic garden is an arrangement of fossil plants in the open, such as may be seen in the Breslau Botanic Garden,¹ where the coal measure series of strata have been built up and characteristic fossil plants have been arranged to form a kind of fossil rock-garden. Such an exhibition as this in close connection with the collection of living plants, is probably of greater educational value than a similar display would be within the four walls of a museum and may be assumed to justify its formation.

How numerous are the possibilities of arrangement in the modern botanic garden has been fully realized by the enlightened botanists of the present day. The difficulty, however, which is being somewhat acutely felt in many institutions, is that of lack of space, not only for the vast numbers of new plants being introduced to cultivation—particularly from China—but also for new and important developments

¹ Göppert, H. R. *Der Königliche Garten der Universität Breslau*, Führer. 1875.

made necessary by the progress of the science of botany both for teaching purposes and for research.

Experiments in plant breeding, for instance, which are a legitimate development of botanic garden research, demand an amount of space which many gardens are unable to afford, and in the tropics in particular such work has had to be relegated to definite experiment stations. In England work of this character is being carried on mainly in connection with agricultural institutions and at the newly-founded John Innes Horticultural Institution at Merton, under the direction of Mr. Bateson, while in the United States such lines of inquiry are being pursued with laudatory vigor by the United States Department of Agriculture and by many other public and private institutions.

Another function of botanic gardens of first importance is the opportunity they afford for the training of men; and in work of this character Kew has probably played a larger share than any other garden. From Kew, in the course of her long history, her sons have gone out either as collectors or gardeners to bring home plants of interest and of economic value, or to take charge of the botanical establishments in the British Colonies and Dependencies. A glance at the Kew roll will also show how many of her young men are helping to propagate the art and science of horticulture in the United States of America.

With some of our larger institutions one of the most important functions in the past has been the distribution of plants of economic importance. The distribution of cotton seed, in 1732, by Philip Miller from the Chelsea Garden to Georgia (the parent stock of upland cotton), the introduction of Para and other rubber plants, and of *Cinchona* from South America through the agency of Kew, of tea into India by the Calcutta Botanic Garden, may be cited as a few among innumerable cases. There are those who have expressed the opinion that this function of botanic gardens is now obsolete, but it does not require much reflection to perceive how wide is the field of usefulness still open in the direction of the introduction and distribution of plants.

Our smaller botanic gardens then may rest content with the attempt to develop their resources on lines best calculated to stimulate interest and promote sound learning, both as centers of education and of research, while it falls to the lot of the larger institutions to display as far as possible the complexity and variety of the vegetable kingdom. The latter, with their herbaria, museums, and laboratories, are responsible to the world for the correctness of the information they supply, since in cases of economic plants incorrect determinations or injudicious advice may involve incalculable harm to the planting community, whose interests they serve.

The magnitude of this responsibility has been fully appreciated, and the results achieved amply serve to demonstrate the success which has attended the efforts of the distinguished botanists who have guided the destinies of our botanic gardens.

“The people will tell of their wisdom and the congregation will shew forth their praise.”

BOOKS AND PAPERS RELATING TO BOTANIC GARDENS

1. Amherst, Hon. Alicia. A history of gardening in England. London, 1896.
2. Britton, N. L. Botanical gardens. Bull. Torr. Bot. Club 23: 331-345. 1896. Also in N. Y. Bot. Gard., Bull. 1: 62-77. 1897.
3. De Candolle, A. P. Notice abrégée de l'histoire et l'administration des jardins botaniques. Dict. d. Sci. Nat. 24: 165-181. 1822. (Unfortunately this account has not been seen.)
4. Holmes, E. M. Horticulture in relation to medicine. Roy. Hort. Soc., Jour. 31: 42-61. 1906.
5. Johnson, G. W. A history of English gardening. London, 1829.
6. Kerner von Marilaun, Anton. Die botanischen Gärten, ihre Aufgabe in der Vergangenheit, Gegenwart und Zukunft. Innsbruck, 1874.
7. Maiden, J. H. Functions of a botanic garden, etc. Roy. Soc. N. S. Wales, Jour. and Proc. 46: 1-73. 1912. [See pp. 49-73.]
8. Philippi, F. Los jardines botánicos. Santiago de Chile, 1878.
9. Pulteney, R. Sketches of the progress of botany in England. 2 vols. London, 1790.

EXPLANATION OF PLATE

PLATE 4

Padua Botanic Garden.

Photograph of plate in de Visiani's 'Dell' origine ed anzianita dell' orto botanico di Padova.' Padua, 1839. (See p. 191.)



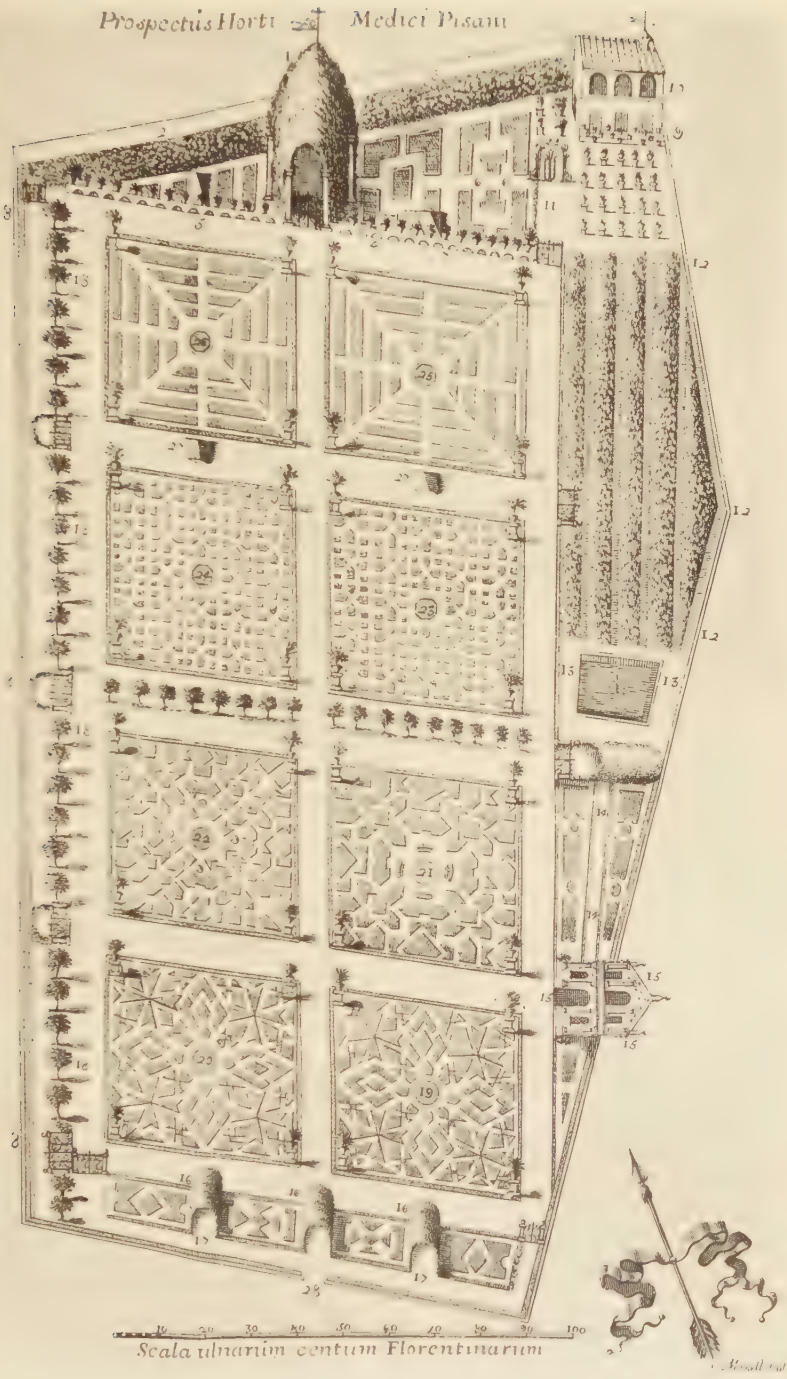
HILL—BOTANIC GARDENS

EXPLANATION OF PLATE

PLATE 5

Pisa Botanic Garden.

Photograph of plate in M. A. Tilli's 'Catalogus Plantarum Horti Pisani,' Florence, 1723. (For explanation see p. 192.)



HILL—BOTANIC GARDENS

EXPLANATION OF PLATE

PLATE 6

Photograph of title page of Gerard's 'Herball.' 1597. (See p. 196.)



HILL—BOTANIC GARDENS

EXPLANATION OF PLATE

PLATE 7

Photograph of title page of Parkinson's 'Paradisi in sole Paradisus
Terrestris.' 1656. [2nd ed.] (See p. 197.)

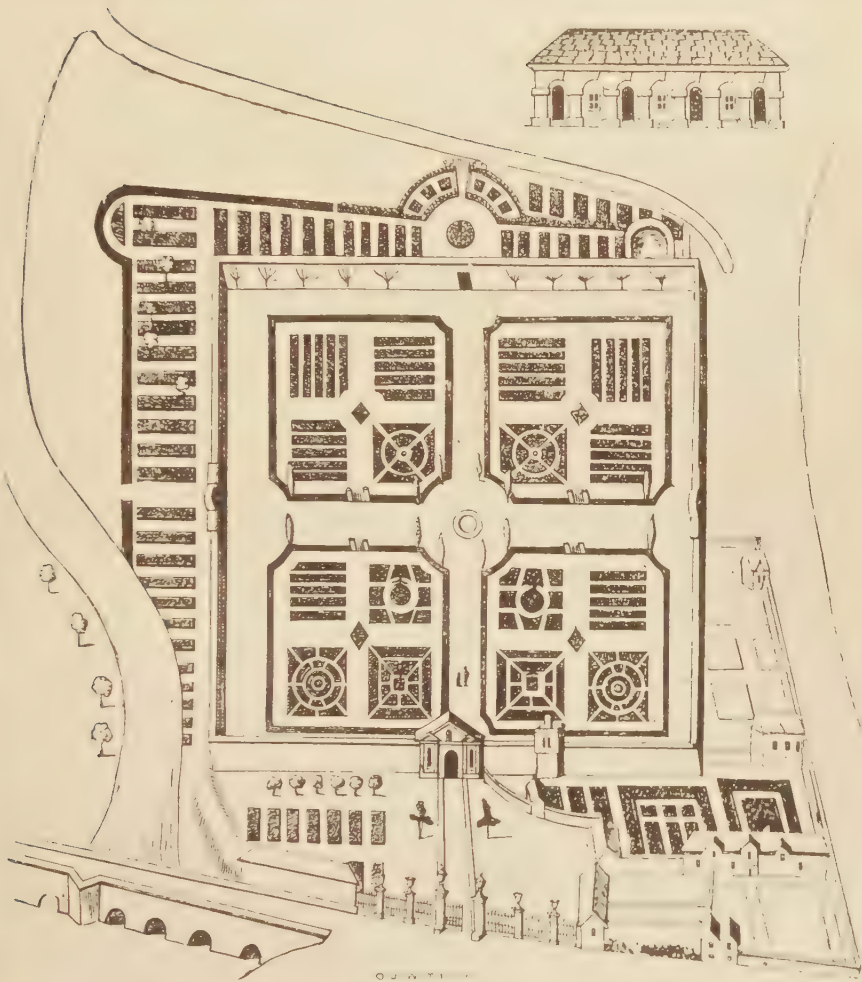


EXPLANATION OF PLATE

PLATE 8

The Oxford Botanic Garden, founded 1621. Reproduced from Logan's plan of the Garden in 1675. (See p. 197.)

South Elevation of the Conservatory



East Bridge

EXPLANATION OF PLATE

PLATE 9

Royal Botanic Gardens, Kew, showing dates and extent of successive additions to the area open to the public and site of the original Botanic Garden of 1760. Photograph of plan in W. J. Bean's 'The Royal Botanic Gardens. Kew,' London, 1908. (See p. 206.)—Published by permission of Cassell & Co., Ltd. London, England.



HILL—BOTANIC GARDENS

EXPLANATION OF PLATE

PLATE 10

The Herbaceous Ground, Royal Botanic Gardens, Kew, showing beds arranged according to the natural orders.



EXPLANATION OF PLATE

PLATE 11

The Rhododendron Dell, Royal Botanic Gardens, Kew.



EXPLANATION OF PLATE

PLATE 12

The Lake, Royal Botanic Gardens, Kew.



HILL—BOTANIC GARDENS

RECENT INVESTIGATIONS ON THE PROTOPLASM OF PLANT CELLS AND ITS COLLOIDAL PROPERTIES

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I have the honor of publicly congratulating the Representatives of the Missouri Botanical Garden upon the Twenty-fifth Anniversary of Henry Shaw's magnificent foundation,—the unique memorial of a magnanimous citizen of this great metropolis.

I shall endeavor to show to the members of this splendid assembly how plant physiologists at present attempt to reach a satisfactory understanding of the wonderful mechanism which in never-ceasing variation is unfolded to us in myriads of phenomena characteristic of nutrition, reproduction, adaptation, growth, and stimulation, in the lower as well as in the higher plant organisms.

Wherever science is following these various processes to their mysteriously hidden roots, the physiologist has to face the complex problems associated with the living content, the so-called protoplasm of the plant cell. Without this singular matter plant cells are mere dead bodies able neither to grow, to take up food, nor to assimilate their nutriment.

It was not until 1841 that Hugo von Mohl, the well-known botanist of Tübingen, discovered the important fact that all phenomena in cell life are strictly confined to the thin layer of slimy material which clothes the inside of each growing and living plant cell. He stated that this protoplasmic slime was stained deeply yellow by means of iodine, and he expressed the opinion that protein substances in particular were the constituents of this living material, from which all other parts and organs of the cell were believed to take their origin.

We shall not be surprised to learn that biologists felt inclined to suppose that the protoplasm might contain some

peculiar and highly complex proteins constituting the living matter in the proper meaning of the word, whose chemical qualities we should have to make responsible for the whole complex of life phenomena. Therefore, it appeared a most attractive problem to subject protoplasm to a thorough chemical investigation. The names of Reinke and Rodewald are connected with this work. These two botanists, in 1880, then in Göttingen, analyzed the protoplasmic mass, the so-called plasmodium, of *Fuligo septica*, a common species of the *Myxomycetes*. The result was that a part, about three-quarters, of the material was recognized to belong to the protein group in the widest sense; while 25 per cent was a mixture of diverse carbohydrates, fatty bodies, organic acids, and inorganic materials. No evidence of the presence of any peculiar protoplasmic substances was found. Reinke, therefore, laid emphasis on the point that protoplasm could not be regarded as a single chemical body of peculiar qualities, but that it should be considered as a mixture of various substances, of which not even one was unknown to the chemists. The consequence of this view was that Reinke inclined to the hypothesis that the peculiarities of protoplasm were not due to its chemical nature but rather to its peculiar structure. The stuff-hypothesis had to be replaced by a structure-theory of protoplasm.

At present, however, we can scarcely accept all conclusions drawn by Reinke from his famous analysis of protoplasm. Reinke thought that all the vital properties of living protoplasm were destroyed when cells were killed, in the same way as the mechanism of a watch is destroyed by grinding it down in a mortar. The chemical substances, however, may remain unchanged while the mechanism is forever destroyed. The first experiments which proved that Reinke's simile is not quite an exact one were obtained from studies on the various enzyme effects which continue in a mass of finely comminuted tissue. Among those effects we know a series of processes which undoubtedly belong to the complex of vital metabolism,—as, for example, to those of respiration and digestion. And these effects may be followed for weeks and for months after

trituration of the cells, if precaution is taken to prevent change in the material by bacterial action. But the essential difference between such autodigestion and the life-process consists in the fact that the first is not ruled by the laws of correlation and regulation, which are so peculiar to life processes. Nevertheless, we cannot say that the whole of the life-mechanism is destroyed by grinding down living organs. At least a part of it cannot immediately be transformed by this type of disintegration. From this we may draw the conclusion that there are certain chemical substances present in protoplasm which are responsible for certain activities of the living tissue. Such substances are the enzymes, which are entirely unknown in inanimate nature, and absolutely distinctive of cell protoplasm. Further, we cannot suppress some scruple that in Reinke's analysis there were examined not the original protein-bodies of protoplasm, but only substances artificially produced during the treatment of the original material.

Our chief objection against the "Engine-Theory" of protoplasm is that no mechanism has hitherto been known which may be destroyed by heat as easily as is protoplasm, whilst on the other hand one cannot immediately and entirely destroy it merely by pounding to an impalpable pulp. Besides this, recent investigations on the proteids of animal organs—in which great care was taken to dry the pulp quickly at a temperature as low as possible—have shown that there really exist highly compounded protein bodies of hitherto unknown constitution which have to be considered as real constituents of protoplasm.

Can such discoveries in some way explain the vital properties of the cell? It seems as if we may not understand the wonderfully accurate working-together of all organs in cells without supposing trans-microscopical structural qualities; but we need not assume any mysterious new forces or structures. Most of the well-known characteristics of protoplasm can be understood by considering further the colloidal state of the constituents of the cells.

The first naturalist who turned his attention to the great importance of colloidal substances in cells was Bütschli, the zoölogist of Heidelberg. A great number of his admirable papers deals with the microscopical features of cell plasma, which he described as a framework of jelly-like substances containing interstices, or meshes filled with fluid substances. Bütschli emphasized the view that the foam structure described by him is not peculiar to living matter, because a mixture of oil and gelatin solution shows the same microscopical structure which he attributed to protoplasm and to all colloids.

But later on it became more and more probable that such a foam structure in protoplasm indicates nothing more than certain gross features which are by no means identical with the real colloidal structure of plasmatic constituents. Not even in gels, or solid colloids, apparently, is the foam structure a dominant characteristic. Zsigmondy's recent work on gelatinous structure clearly showed that while forming the gel the colloidal particles, which are distinctly visible in the ultra-microscope, do not arrange themselves in a network, but settle quite irregularly; so that we cannot assume that meshes are formed in the precipitation of colloids. On the other hand, biologists of rank, as Lepeschkin, after a careful study of the microscopical structure and the physical properties of protoplasm, have arrived at the conclusion that we should not regard it as a foamy mass, or jelly-like substance, but rather as a liquid colloid with the characteristics of protein sols of certain higher concentrations. We can easily confirm the observation that protoplasm, examined by means of the highest power of the microscope, often appears merely as a homogeneous liquid, or transparent mass, sometimes moderately turbid from the presence of small distinct drops or corpuscles which are collectively known under the name of "microsomata." Even though we do not accept Bütschli's idea with respect to specific structure, we fully share his more general point of view that living protoplasm owes its peculiar activities to colloidal qualities. And this represents our attitude to-day towards protoplasmic investigation.

The chemistry of colloids is not a descriptive science. To the utmost extent it has to use experimental physical methods. So we cannot advance in knowledge of protoplasm by mere microscopical observation, but mainly by experimental investigation.

A long time even before colloidal chemistry became dominant as the basis for the physiology of protoplasm, a memorable epoch in plant physiology had opened, developing from the ingenious work of Pfeffer and De Vries on the osmotic properties of living cells. These investigations unveiled the fundamental fact that living protoplasm alone is in possession of those peculiar properties of permeability which are responsible for the whole complex of nutrition. Dead protoplasm behaves quite differently. Since, however, differences in respect of the penetration of different solutions can be detected to a certain extent in colloidal membranes, it became probable that the so-called semipermeability of living protoplasm is a colloidal phenomenon, due to the constituent colloids in living protoplasm; whilst after the death of the cells the coagulation of these colloids completely changes the peculiar permeability of the protoplasmic layer.

It was, however, Ernest Overton, in 1899, then at Zurich, who acquired the merit of placing colloidal chemistry in fundamental relation to the phenomena of diosmosis in living cells. The well-known theory of Overton consists in the hypothesis that fatty substances play an important rôle as constituent elements in the protoplasmic matrix. It is due to such substances, generally comprised under "lipoid bodies," that living cells show quite distinctive diosmotic qualities. Overton's hypothesis is founded upon the fact that only those substances which readily dissolve in fatty oils are easily diffusible in living cells; whilst all substances which are insoluble in oily media, as sugar or mineral salts, easily produce plasmolysis, because they penetrate into cells only very slowly.

The leading physical idea in this theory was the so-called "Partition-Rule" of Berthelot and Jungfleisch. This law states the fact that there exists a constant relation between the quantities of a certain solute dissolved in two immiscible

solvents. Overton considered the endosmosis of dissolved substances into living cells as merely a question of solubility. It is known how fertile this idea has proved in physiology, particularly in the phenomenon of narcosis, where it is still the leading hypothesis in animal physiology.

But recently experimental work, including my own, has shown that it is scarcely quite correct to consider the endosmosis of solutions into living cells as a typical solution phenomenon. According to Loewe even the partition of methylene-blue or of chloroform between oil and water cannot readily be explained by means of the principle of Henry and Berthelot. Rather, the oily solution of such substances is not a true solution, but only a colloidal solution; so it is not ruled by the laws of osmotic pressure, but by the laws of adsorption.

A striking fact was discovered by Traube and by myself in studying the effects of alcohols and other capillary-active substances on living cells. Their injurious action clearly and exclusively depends upon the relative capillary activity. Every one of these substances kills the cells at a concentration corresponding exactly to a certain value of surface tension. The main importance of this observation consists in the evidence that in narcotic effects capillary phenomena must be a dominant factor. This cannot be interpreted by the supposition that the entrance of narcotics into cells is due to true solution phenomena. The observed capillary effects distinctly show that the factor of real moment is to be found in alterations of contact-surface; but such surface-phenomena are met with only in colloids and in their adsorption.

A prominent feature of our experiments involves the fact that cells of higher plants are constantly killed by concentrations of narcotics such that the capillary activity reaches about two-thirds of the surface tension of pure water in contact with air. It is remarkable that saturated and neutral emulsions of triolein or other typical fats always show approximately the same surface tension value. This result I tried to explain by means of the hypothesis enunciated in the following sentences: Alcohol and other narcotics are taken up by ad-

sorption into living protoplasm. According to the theorem of Willard Gibbs the surface in liquid systems which consist of different fluids and contain some capillary-active substances is always occupied by those substances which show the greatest reduction in the surface tension of the medium. If subsequently another substance with greater capillary activity is added to the system it displaces all other substances from the surface. Narcotics may displace certain plasmic substances in an analogous way, provided that the surface tension of the concentration applied is just a little lower than the surface tension of the plasmatic substances referred to. The fact that the fatal narcotic pressure value coincides with the maximum surface tension in fat emulsions may be explained by the hypothesis that fatal effects of alcohols on living cells consist in destroying the emulsion structure of protoplasm, by displacing some fatty substances. So our experiments to a certain extent uphold the view that the surface layer of protoplasm really contains fat, and thus far is in accordance with Overton's hypothesis.

In the course of time the lipoid-theory of Overton has met with sharp criticism. Among other renowned physiologists, Ruhland strongly denied the presence of fatty bodies in the plasmatic membrane of plant cells. On the other hand, we are aware that animal physiologists, such as Fühner, Höber, and Vernon still firmly adhere to the old lipoid-theory. However, since according to Overton sugars and mineral nutrient salts are believed to penetrate only poorly into the living cell, it is obvious that Overton's hypothesis stands in direct contrast to the common experiences in respect to plant nutrition. The substances referred to are materials which the cells have to take up as among their most important nutrients. Nevertheless, there have been developed some supplementary theories which permit us to lessen the difficulties of the lipoid-theory, for example, that of Nathansohn, according to which the lipoid membrane of protoplasm is not a continuous film of fat, but a kind of mosaic of fat and protein which is able to permit the penetration of both fat-soluble substances and mineral salts.

Ruhland's experiments especially were not at all favorable to the lipoid-hypothesis. They show decidedly the error of the opinion that only those aniline dyes penetrate into living cells which are soluble in oil. Many aniline dyes have been found which are easily taken up by cell protoplasm in spite of their insolubility in fat, while other coloring matters which easily dissolve in fat do not penetrate at all through the living plasmatic layer. Ruhland, as well as Küster, drew from such experiments the convincing conclusion that substances readily soluble in lipoids may not always be readily taken up by the living cells. But in other respects it seems as if Ruhland had gone too far when he denied that protoplasm possesses any fat content. He emphasized that he never could detect any microscopical trace of plasmatic substances which may be stained by means of such aniline dyes as are readily stored by fat.

Since our own experiments seem to be in some accord with the view that fatty matter really is present in protoplasm, I wanted to compare some chemical systems which are entirely free from fat with protoplasm in respect to its behavior toward alcohols. It could be taken as a proof of the view that protoplasm does not contain fatty bodies, if there were noticed no difference between the effects of alcohols on the physical properties of such systems and on protoplasm. The investigations of Mr. Geo. H. Chapman in our laboratory were begun in order to examine the influence of different narcotics on enzymes. Surprisingly, the results were opposed to the above-mentioned view of similar action with respect to these systems. This work clearly showed that the capillarity-rule which is so distinctive of the effects of narcotics on living protoplasm does not apply to the effects of narcotics on enzymes. While the deleterious influence of methyl, ethyl, and propyl alcohol gradually increases with the molecular weight of these homologous substances, the higher members such as butyl and amyl alcohol act considerably less on enzymes, and both heptyl and octyl alcohol have practically no weakening influence on these ferments. In respect to their coagulation by diluted alcohol protein solutions show relations corresponding to

those just discussed. In consequence of this result we can hardly explain the effects of narcotics on protoplasm by the view that only plasmatic protein bodies are influenced by such toxic agents. Besides this, for the coagulation of protein bodies there is required not less than five mols of ethyl alcohol while a little more than two mols is sufficient to kill living protoplasm. Therefore, some other substances in protoplasm besides the protein bodies must be affected by the alcohols, and these substances must differ from the latter in their physical properties. So it seems that the view according to which the plasmatic membrane is constructed exclusively of hydrocolloids, viz., proteins, as Ruhland believes, cannot be considered to be quite satisfactory. Our attention must be directed anew to the possibility that some lipoids play the part of important constituents of the protoplasmic membrane.

On the other hand, I have to state that several lines of experimental work have led us to the conclusion that the endosmose of solutions into living cells never does take place by way of plasma lipoids, but only through hydrocolloidal constituents of the cell plasma. The work of Mr. Krehan, which dealt with the influence of highly diluted hydrocyanic acid on plant cells, distinctly showed that in the presence of this agent the permeability of cells to certain salts, such as sulphates, and to sugar, is raised, so that the threshold of plasmolysis for these substances is raised. When the effects of different salts on plasmolysis were compared it became manifest that just those salts causing the greatest rise of the plasmolytic limit, are those which were strongly adsorbed, and which display a most marked effect on the precipitation or coagulation of albumen. Such salts are sulphates, citrates, tartrates—by their anionic effects, and the salts of ammonium, calcium, and magnesium—by their cationic effects. These phenomena are only to be understood upon the supposition that hydrocolloids are the media through which different substances must pass when taken up by the living cell plasma. There has been discovered not the faintest indication that

lipocolloids can play an important part in endosmose, as Overton originally suggested.

If there really are plasmatic lipoids present, they probably have no significance as the path of nutrient substances into cells. But, on the other hand, lipoids certainly participate in narcotic effects, because the more soluble is this narcotic in fat the more of the narcotic substance is stored by the plasmatic substances. Consequently, the higher members of the series of alcohols are more injurious for cells than the lower, because the lipid constituents of protoplasm become saturated with the narcotic and can discharge these narcotics only slowly. So the protoplasm succumbs to the influence of the narcotic agent. On this point I share the opinion of Böeseken and Waterman.

The capillarity-rule can scarcely be explained otherwise than by the hypothesis that lipoids are present in the surface layer of protoplasm. So we are forced to continue our work as an exploration designed to determine if lipocolloids are present in protoplasm. A plan was devised and a decision was sought in the following manner: Emulsions of pure triolein or of olive-oil were prepared which had about the same surface tension value as have solutions injurious to protoplasm. To a series of samples arranged from such a fat emulsion alcohol in gradually increasing amount was added. The question now was whether there were effects produced on the emulsion in some way comparable to the action of alcohol on cells. Cell plasma contains also protein bodies and mineral salts. So our model of emulsion had to be compounded by adding a solution of mineral salts, as a physiologically balanced mixture, and by adding also albumen solution. The mineral salts were added as in the Van't Hoff mixture in 0.1 molar concentration. An alkali is indispensable, so that 0.1 mol of sodium carbonate was used in order to produce a fine and stable emulsion upon shaking the mixture with oil. The results were in brief the following: When a fat emulsion from olive oil was prepared by mixing only oil, water, and sodium carbonate, the decomposing effect of alcohol on the emulsion was noticed at a concentration of 3 mols, i. e., about 15 per

cent. When concentrations higher than this were used then the emulsion, examined capillarimetrically, did not differ from a mixture of pure alcohol and water of the same concentration (but without oil). Then we added to the emulsion Van't Hoff's solution 0.1 mol instead of water. The decomposition of the emulsion by ethyl alcohol was now observed at 2 mols, i. e., about 10–11 per cent. This is just the concentration of alcohol which kills cells of the higher plants. The addition of sodium chloride 0.1 mol instead of Van't Hoff's liquid showed the critical concentration of alcohol to be 3 mols, about the same concentration as in the absence of mineral salts. On the other hand, the addition of magnesium chloride induced the fatal effect of alcohol at 1 mol, much lower than in living cells. Magnesium sulphate showed the same effect as magnesium chloride, and the sulphate of sodium the same as the chloride. Therefore, it does not seem probable that the differing solubility in alcohol is responsible for the various effects of the salts. One may endeavor to explain these phenomena in the following way: Emulsions are only stable when the droplets of the emulsified fat remain suspended in a soap solution of approximate concentration. Substances which alter the limiting surface between the soap solution and the suspended oil must prove fatal as soon as their capillary activity surpasses the capillary effect of the soap solution. Bivalent cations, such as Mg and Ca, which form insoluble salts with fatty acids, lower the concentration of soap, so that alcohol must exhibit a decomposing action on the emulsion, even in lower concentrations.

From such experiments it seems as if the critical concentration of alcohol for living cells would not be so sharply determined by proteins contained in protoplasm as by the mineral salt and the lipid constituents of the protoplasm. Since we suppose that the various mineral salts in protoplasm are present in about the same concentration as they are found in sea water, or as they are mixed together in Van't Hoff's solution, we have to face the question whether the destructive effect of alcohol on living cell plasma consists in some decomposition of colloidal fat emulsoids in protoplasm.

That protein bodies are not primarily affected by alcohol and other narcotics seems to be sufficiently proved by the fact that ethyl alcohol coagulates protein solution at a concentration not lower than 5 mols, and that while the higher alcohols show fatal effects on living cells, they do not produce any protein coagulation.

So we are brought, I think, by several facts to the conclusion that living protoplasm must be considered as a colloidal emulsion of lipoids in hydrocolloidal media, the latter containing proteins and mineral salts. For the endosmotic passage of dissolved substances the fatty constituents of protoplasm have no significance. The narcosis, however, and the deleterious effects of alcohols clearly show how lipoids, more than the protein constituents of the surface layer of protoplasm, participate in such phenomena. The more we advance in the disclosure of the details regarding colloidal mixtures and structures in living protoplasm, the more indispensable it is to be reserved when applying the new results to the various problems to which an approach is so tempting to the physiologist.

Many may feel inclined to be disappointed when they observe how much time and mental energy are needed to study only so small a question as that about the presence of fat in protoplasm. But now after some years' work on this subject it may be seen how important a part is to be attributed even to the combination of mineral salts contained in the plasma colloids. And so we may hope that in the progress of research new and unexpected paths may become visible and open to the indefatigable investigator. Further, we shall not be discouraged if when after long and patient work some results and ideas are won which subsequently are proved untenable. We are all common soldiers in the great battle for truth in science, and we know that few will attain the happiness of planting the flag of victory upon the battlements of the conquered fortress.

THE EXPERIMENTAL MODIFICATION OF GERM-PLASM

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The doctrine of an inviolable germ-plasm has formed the foundation of many imposing edifices in biological thought, and facilitated many advances in genetics and heredity during the last two decades. The authors who have rigidly adhered to the principles of the hypothesis and reasoned from its tenets have exposed many fallacies which have been offered in explanation of problems in evolution.

This prevalence of theoretical considerations over mistaken experiences has laid the foundation for an unreasoning devotion to the idea of an independent germ-plasm, carrying agents which may not be seen, measured, or tested in any practicable manner, and which might consequently be termed "idealo-plasm" with attributes approaching the supra-physical.

The desperate straits of those who voluntarily consign themselves to the bondage of such a conception is well exemplified by the group of writers who subscribe to the conclusion that all evolutionary movement is due simply to recombination and rearrangement of qualities or factors already present in the protoplasm. An additional illustration of the futile extremes to which this view may be pushed is to be found in the recent utterances of Bateson, who has arrived at the conclusion that evolution is mainly and essentially loss of inhibitors, and release of activities previously latent or suppressed, an hypothesis which predicates premutation.

If it be allowed that the non-appearance of a character is a direct loss of its determiner and that the appearance of a new feature is the loss of a retarder or inhibitor which held it in abeyance, then the answer to the question as to the method by which organisms have arrived at their present condition is obvious, but of a simplicity that is metaphysical instead of actual and hence of little value, even tentatively, as a frame-

work on which new concepts in biological science may be formulated. The group of problems with which we are endeavoring to make headway are in the domain of physiology and their solution may be reached only by experimentation, the results of which are to be interpreted in terms of physico-chemical activities and their correlated functional manifestations in the living organism.

That phylogenetic advance in the main lines of descent in the plant kingdom at least reflects, or harmonizes with, the expectancies of somatic experience is tacitly admitted on all hands, but that the direct response of a shoot to the environment, or conversely stated, that the impression on the soma made by environic agencies is communicated to successive generations in a constant manner has not been demonstrated, although it seems fairly established that certain experiences of individual plants are reflected directly or indirectly to the next generation, and in lesser degree to the next or second generation. How are lasting or permanent changes brought about?

Functional adequacy and architectural suitability present themselves on every hand, yet about all of our reliable evidence is against anything like a direct or functional adaptation becoming hereditary or continuously transmissible.

Two methods of experimental attack on the problem are available. Species showing measurable features and of simple genetic constitution may be taken from their habitual or known environment to other localities in which the climatic and soil characters may be calibrated and the response of the organism, somatically and hereditarily, determined. Hundreds of thousands of introductions and acclimatization operations have been carried out in agriculture, horticulture, and especially in botanic gardens during the last century, yet neither the genetic constitution nor the response of the organism has been followed by trained observers who compared the plants in their different habitats. The exposure of the organism to any climatic complex, of course, might affect the germ-plasm directly, and any departure detected in such experimentation must be evaluated by controlled cultures under

laboratory conditions in which both the nature of the reaction and the identity of the inciting agent may be found. The most notable series of experiments of this character which have as yet been carried out are those of Tower with the potato beetles.

Over two hundred species of seed-plants selected for their suitability and promise of response have been taken into the series of cultures of the Department of Botanical Research on mountain top, desert, and at the sea-shore, less than eighty of which have survived and about a score continue in all three locations. The most notable feature in the behavior of these plants put under stress in unaccustomed habitats consists in divergences in sexual reproduction and seed-formation. Conjointly with this decrease of the sexual reproduction, vegetative propagation assumes a greater importance. Shoots are variously affected. The measurement of these departures and their fate when the n th generation is returned to the original habitat, or to a place in which the habitat tension is changed, will be necessary to determine whether or not permanent impress on the species has been made.

The second method would include all forms of experimentation in which inciting agents would be applied directly to the reproductive bodies, in which case any deviation from the usual or typical would be more clearly attributable to changes in the germ-plasm.

It is pertinent to call attention to the necessity for new viewpoints and new standards in the evaluation of any results which may be obtained in such manner. We are not likely to go far or progress easily into the region of the unknown if we attempt to interpret these effects too directly, with the idea that determiners, inhibitors, genes, etc., are ultimate or even penultimate units. In brief, the time has come for testing the performances of lineal series of organisms by methods in which attention will be centered upon the physico-chemical complex and an open eye will be kept for cleavage lines which may cut across directly or obliquely the limits of all of the arbitrary concepts of alternate inheritance. The house of the living thing is inclusive of walls, doors, roofs, windows, floors,

ceilings, rafters, and plumbing, but the materials used may be bricks, stones, metals, sand, lime, boards, glass, and paint. Our present needs lead us to experiments with these components rather than to trials of the possible combinations and inhibitions, possibilities and impossibilities of sets of builders' blocks, no matter how complete or full these may be.

Living material is a colloidal complex with its enmeshed reactions highly fluctuant, its combinations unstable and its types of energy transformation multifold. It is concrete, however, and amenable to experimentation of many kinds. Its physical qualities and form undergo changes of phase which have some correspondence with the mechanism of morphogeny, reproduction, and heredity. Thus, for instance, in the higher plants the germinal protoplasm in the earlier stages of the individual is in the form of meristematic tracts made up of highly distended plasts in which absorption of water, hydration, auxetic enlargement, and division of the separate elements is very marked and rapid. Elements at the peripheries of these masses are separated which undergo differentiation and pass into the permanent tissues of the individual. These separating cells may be modified to an enormous extent by external agencies; thus conditions of aridity acting upon an individual may cause the tissues formed from its embryonic tracts to make such structures as to give the organs which they make up a xerophytic aspect.

This final xerophytic or other character of the soma, however, is in the permanent tissue, and the modifications which have resulted in its specialization ensued after the cells were pushed away from the meristem, and there seems to be no reflection of the final fixed qualities back to the embryonic tract, although there are many promising possibilities to be considered. Of these none are more interesting than the regenerative processes by which highly specialized cells reassume embryonic activity and reproduce members or individuals vegetatively. Actual tests of the transmission and permanence of the specializations under these conditions have not yet been made with that exactitude which would allow any serious conclusion to be formulated. At certain stages of the

ontogeny, generally much later in the plant than in the animal, and this is a matter which may be determined by the environic agencies, the germ-plasm or meristem tract undergoes such change of phase that instead of all of its separating elements passing into somatic cells a few become reproductive masses from which sexually specialized elements may be differentiated, and in which the number of chromosomes, the metabolic balance, degree of hydratation, auxetic energy and mechanism of division suggest physico-chemical conditions widely different from those of somatic elements; furthermore, the reproductive elements are highly individualized. The meristem in its myriad cells may at any moment present all of the phases of growth and differentiation. The egg nucleus or the fertilized egg, a single element of the plasma, may include the fate of the individual and its unending line of progress, and it may be affected in its entirety by agencies impinging upon it. The reaction of such specialized cells to external agencies would of course be different from those of the meristem tracts, which are made up of plasmatic units of the most generalized form.

The experiments of Tower with the *Leptinotarsae*, which have been carried on under widely diverse conditions in southern tropical Mexico, in the arid semi-tropical climate of the Desert Laboratory, and under controlled conditions at the University of Chicago, furnish a great series of cultures of these beetles in which it is possible to demonstrate logically by exclusion and analysis that certain climatic features, notably moisture, may affect the germ-plasm, or the entire organism when the germ-plasm is in a certain stage, in such manner as to induce disturbances in hereditary lines. These experiments show the vulnerability of the germ-plasm.

That the germ-plasm is directly responsive to the action of foreign substances which are introduced into the embryo-sac was demonstrated when (early in 1905) I was so fortunate as to hit upon an experimental method of treatment of the ovaries of seed-plants which resulted in the formation of embryos developing into individuals not entirely identical with the parental types. The essential feature of the discovery

consisted in the successful introduction of various substances into the neighborhood of the embryo-sacs at the time that fertilization was imminent, and when the first trials were made I had two main purposes in mind: first, to ascertain whether or not foreign substances could be introduced into ovaries in such manner as to affect the ovules with a minimum of traumatic effects, so that the ovaries might reach maturity; and secondly, to ascertain whether or not such changes could be produced in an early stage of sexual specialization, before the development of the embryo-sac or after the union of the sexual elements in fertilization.

The first results were obtained with pure strains of *Oenothera biennis* and *Raimannia odorata* at the time mentioned, but the transfer of my activities from the New York Botanical Garden to the Desert Laboratory made it impossible to carry out cultures of the progeny or to repeat similar experiments upon this material. Meanwhile, Col. R. H. Firth, of the Royal Medical Corps of Great Britain, duplicated¹ my general results with *Raimannia* and other plants in 1908, although the fact that I had previously done this work was unknown to him.

New material was selected from the vicinity of the Desert Laboratory and the tests were begun anew in 1906. The difficulties to be overcome in such experiments are fully commensurate with the importance of the problem upon which they bear. It is a necessary preliminary that the plants chosen for the operations should be an elementary strain, a matter which may need two or three years for determination, if not already known. Next, not all ovaries will withstand the shock and injury inflicted in the operations. The chances of ultimate success will be greatest in many-seeded ovaries in which the number, however, does not extend much beyond that of ovules which may be affected by a single operation, giving some opportunity for differentiation of effects and not entailing large cultures. Lastly it is advantageous to deal with perennial species which come quickly to maturity. This gives

¹ Firth, R. H. Roy. Med. Corps, Jour. 16: 497-514. 1911.

the operator opportunity to preserve the original material alive and to have it for comparison with succeeding generations.

The numerous cacti in the vicinity of the Desert Laboratory lead them to be selected for some tests, and the mechanical conditions for operation which they offer are unexcelled. As much as 1 cc. of solution may be introduced into the ovary of an opuntia without traumatic effects, but as all are under suspicion as to their genetic complexity, and as they germinate and develop slowly, the investigator must wait the greater part of a decade to obtain decisive results. Striking departures were obtained with *Echinocereus Fendleri*, a small cylindrical form native to southern Arizona, and the changed characters grouped in one derivative have not been obtained in nature or in cultures of the original. This derivative has been obtained a second time. The species, however, presents such a complexity of characters that definite conclusions are difficult.

Similar conditions were encountered in *Penstemon Wrightii*, about which an announcement was made in 1909. Some of these, however, furnished material from which the greatest sources of error might be eliminated.

The search for suitable subjects for experimentation was continued and the results with *Penstemon* led to a closer examination of other members of the *Scrophulariaceae*. Finally, an undescribed species of *Scrophularia* from the pine-forest area on the Santa Catalina Mountains in Arizona was brought into the environic series of the Laboratory of this Department in 1909. Rootstocks were taken to the Coastal Laboratory, and seeds were germinated at various localities. After having seen many hundreds of plants taken from various parts of its range and having followed them thoroughly two and three generations, it was found that the species is a simple one and not readily separable into elementary forms or strains. The only noticeable feature suggestive of complications was the fact that the broad-bladed nepionic leaf-forms are sometimes carried nearly to the summits of stems grown under certain conditions, giving the appearance of a robust race.

Another feature that received attention was the fact that branches formed in the closing part of the cycle of development of shoots bear leaves very much smaller than those arising from the median part of the main stem during the first part of the season. The flowers borne on these branches are also much paler than those on the more robust branches. Peloric flowers sometimes appear near the apices of the inflorescences in this as well as in other species of the genus. It is to be noted also that the divisions of the corolla are variously and irregularly incised on individuals at times during the season, but these are not heritable and do not appear in any regular manner.

This *scrophularia* appearing to offer some promise, several ovaries of a plant at Carmel were treated with solution of potassium iodide, one part in forty thousand, in July, 1911, and the ripened capsules were collected in September of that year. No record was made as to the time of day (see page 268) and nothing may therefore be said as to the possibilities of the action of the reagent on egg or pollen nuclei, singly, together, or after fertilization. No other species of *Scrophularia* grew near the cultures at that time.

The seeds were sown in suitable pans of screened soil, and in February three plantlets had survived. In May these were set in the open and their development followed. One formed a shoot fairly equivalent to the normal, finally producing flowers in which the anthocyanins of the flowers were of a noticeably deep hue. The two remaining plantlets were characterized by a succulent aspect of the leaves, and by a lighter or yellow color of the leaves and stems. Inflorescences were matured late in 1912, and the flowers on one of the derivatives, as they may be called, were so completely lacking in color as to be a cream-white, this derivative being designated as *albida*, while the other showed some marginal color and a rusty tinge, and was designated as *rufida*.

Some disturbance of the relative velocities of development of the fibrovascular elements and mesophyll had taken place in both forms, so that the leaves were variously bowed and convexed and the two halves of the laminae were unequal and the

whole blade was more oblique in outline. The elongation of the lamina had been checked and the ratio of width to length of the leaves was greater than in the parental stock. If correspondent leaves of *rufida* and the originals were laid side by side it could be seen that the basal veins on the side away from which the tips were curved were different in the two cases, the derivative showing two strong veins in the place in which one lateral with a thin branch occurred in the original (fig. 1). The water relations of derivatives and normal were not identical, and when young shoots or branches developed

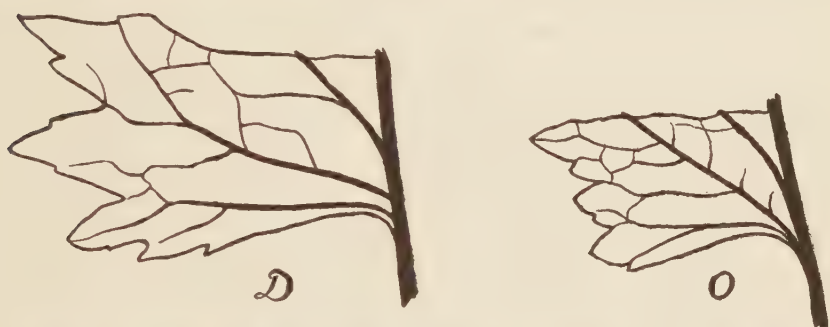


Fig. 1. O, branching lateral vein in parental *Scrophularia*; D, branching vein replaced by two laterals in leaf of modified *Scrophularia*.

under similar conditions were detached, those of the derivatives flagged and wilted much more quickly than those of the normal.

The auxetic departures noted above also extended to the inflorescences, which in the original show a fairly regular basipetal development into thyrses. The derivatives, however, exhibited a rather irregular maturation of clumps of buds and the thyrses were very irregular, not reaching the spread of the parental forms. The fragility of the leaves does not seem to extend to the flowers, which opened very slowly, and in some cases the distended corolla persisted for a few days. The amount of color in the corolla was largely a matter of illumination, but under equivalent circumstances the derivatives always showed less than the parental form. As noted above the color persists to some degree in the deriva-

tives along the margins of the uppermost lobes of the corolla, while that on the broad upper surface disappears. It is to be recalled that it is the color of this region which is variously disposed in other species of the genus.

The corolla lobes were irregularly incised in the flowers of the first and second seasons of the F_1 , as they have been seen to be in the original, but in the second generation of both derivatives cultivated at the Desert Laboratory this effect persists as a regular wedge-shaped incision of the lower lip only, and is not seen in every individual of both derivatives, although the seeds were from plants which may have been pollinated by the parental form.

Seedlings from the original stock grown from seeds gathered on the Santa Catalina Mountains in Arizona were sowed early in 1910 at the Desert Laboratory and the plantlets preserved on April 15 furnished the data:

First pair of leaves smaller than in the derivative, being only 13–15.5mm. wide and 16–18mm. long, obscurely dentate with not more than two or three blunt teeth showing on each side. The petioles were 12–16mm. long. The third pair of leaves above the cotyledons, which probably were not quite mature, had petioles 20mm. long, and laminae 22–25x50–52mm. Marginal stalked glands were so numerous that 15–20 appeared in the field of the microscope at one time, and these structures were very numerous on the petioles. It is to be noted that differences in the last-named feature between this original and the derivatives disappear in the adult, or on the leaves appearing in the later stages.

Seeds from the original two derivatives matured at Carmel late in the summer of 1913 were sowed in the greenhouse at Tucson in November, 1913. But one plant of *albida*, the extremest departure, survived, while four of *rufida* were secured. These, of course, represented the F_2 of the departures. The measurements of *rufida* correspondent with those of the original are as follows: First three leaves deeply incised, five or six teeth on a side, abruptly pointed. Petioles 18–22mm. long, laminae 21–26mm. wide and 41–45mm. long. Mature leaves on sixth, seventh and eighth internodes, with petioles

36–45mm., and laminae 36–56x85–100mm. Marginal glands showing 6–10 in field, few on the petioles.

The single plantlet of *albida* bore leaves, the first pair of which were not deeply cut, the three or four teeth on each side being abruptly but sharply pointed, the petioles 15mm. long, and the laminae 24–26x35–38mm. The leaves from the sixth, seventh and eighth internodes had petioles 30–40mm., and laminae 45–51x90–100mm. Not more than four stalked glands might be seen in the field at any one time. These trichomes were very sparsely distributed over the under surface of the petioles only. The greater relative width of these leaves was correlated with a greater angle of divergence of the lateral veins from the midrib, a feature which, as will be shown later, was to be observed in adult plants.

The three plants representing the progeny of the treated individual were established in a row within a half meter of each other at Carmel in 1912. Irregular clusters of long thickened roots were formed, and these, as is customary with the species, bear buds and are a means of propagation of the plant. The three plants were taken up in November, 1913. While the main clumps could be identified, yet broken fragments of roots were preserved which could not be assigned to any one of the three, and although these were and are still preserved they are not taken into account here.

Albida was divided in May and June, 1914, and portions were sent to coöperators in New York, St. Louis and Chicago, but all failed to survive this unseasonable transplantation, so that at the present time this strain is represented by only two clumps, one of which is at the Desert Laboratory and the other at the Coastal Laboratory. The single plant of *albida* bloomed at Tucson early in the year, while the one at Carmel reached that stage too late to mature seeds.

Rufida was divided into three clumps and reset in the garden at the Coastal Laboratory in November, 1913. The shoots from these began to open flowers in July, 1914, which corresponded in all essential particulars with those of the previous seasons except that they were more highly regular. Two were enclosed in small glass cages for protection and to insure

close pollination, a strong individual of the original being similarly enclosed for purposes of control. Conditions being favorable for a minute comparison of these plants with the parental type, colored illustrations of flowers and buds and diagram of structure were prepared. The inequality of the leaves was recorded by direct prints. The dimensional relations noted above were again seen. The readiness with which the leaves flag was noted and in these organs, as well as in the stems, it was seen that rigidity is maintained by turgidity rather than by stiffness of the mechanical tissues. The development of the bast-fibers is less marked in the derivative,

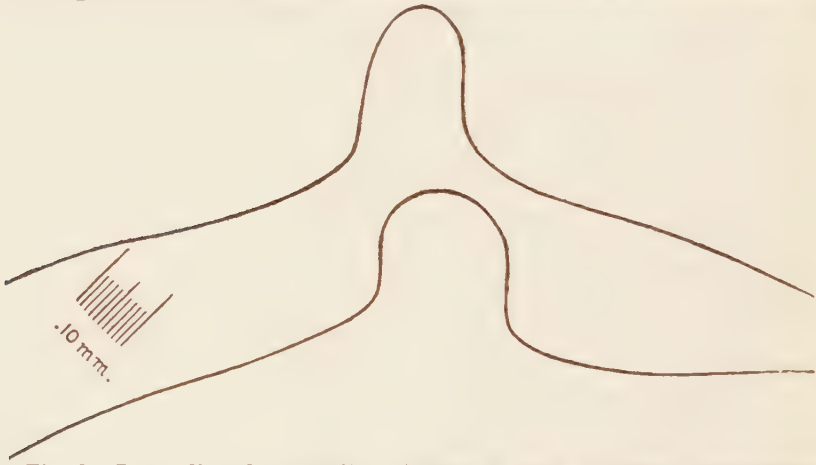


Fig. 2. Lower line shows outline of angle of stem of parent *Scrophularia*; upper line outline of same feature in derivative.

and a similar deficiency of wood-formation is noted. A correspondent difference is apparent in the wings of the angles of the stems, which are thick with their sides parallel in the original, while in the derivative these decrease in thickness gradually toward the margin, with the effect in cross-section seen in fig. 2. The actual value or importance of these differences is not a matter of moment in the present connection. The chief interest lies in the fact that recognizable effects have been produced by the introduction of foreign substances into ovaries and that the differences shown by the first generation, F_1 , are borne by the second generation, F_2 . The original observations with the plant in which this was demonstrated

began in 1909, the treatments were made in 1911, and now first and second generations of the derivatives are alive, as well as the original stock.

Much irrelevant comment and inconclusive experimentation has followed the original announcement of the discovery of the methods used in this work. The necessity for a careful genetic analysis of the material for treatment has already been noted, and it may be well to call attention to some of the features of operation which might appear simple, yet are not easily carried out. No better way has yet been found for introducing solutions into the region of the embryo-sac than by injection into ovaries with an all-glass syringe fitted with gold needles (14 karat). The wounding of the ovary produces abortion in some species, and in almost all treatments some of the ovules are crushed. This, however, is a matter of no moment if some reached by the reagent survive and come to maturity. The extent and mode of diffusion of the reagent is in fact one of the most important features of the treatment, and the experimenter will do well to make control tests for the purpose of finding out whether or not there is some possibility of success.

A test of the ovaries of *Carnegiea* previously described showed that the liquid was taken up by the placental vessels and conducted to a point near the egg cell in a very short time if the reagent were introduced into the ovaries of flowers fully open and mature. Operations made at an earlier stage resulted in the accumulation of the reagent in the inner walls of the locule, in the integument of the ovule and especially at the micropylar orifice. The pollen tube would be subject to the action of the accumulated substance in the micropyle and integument in this case.¹

It being my present intention to extend experimentation in the *Scrophulariaceae*, tests have been made with methylene blue in the ovaries of *Penstemon Torreyi*, the solution being one part of the dye to ten thousand of distilled water.

¹ MacDougal, D. T. Alterations in heredity induced by ovarian treatments. Bot. Gaz. 51: 241-256. 1911.

Three hours later but little of the color could be found in sections of the ovary. Next, five ovaries of *Oenothera* 3.21

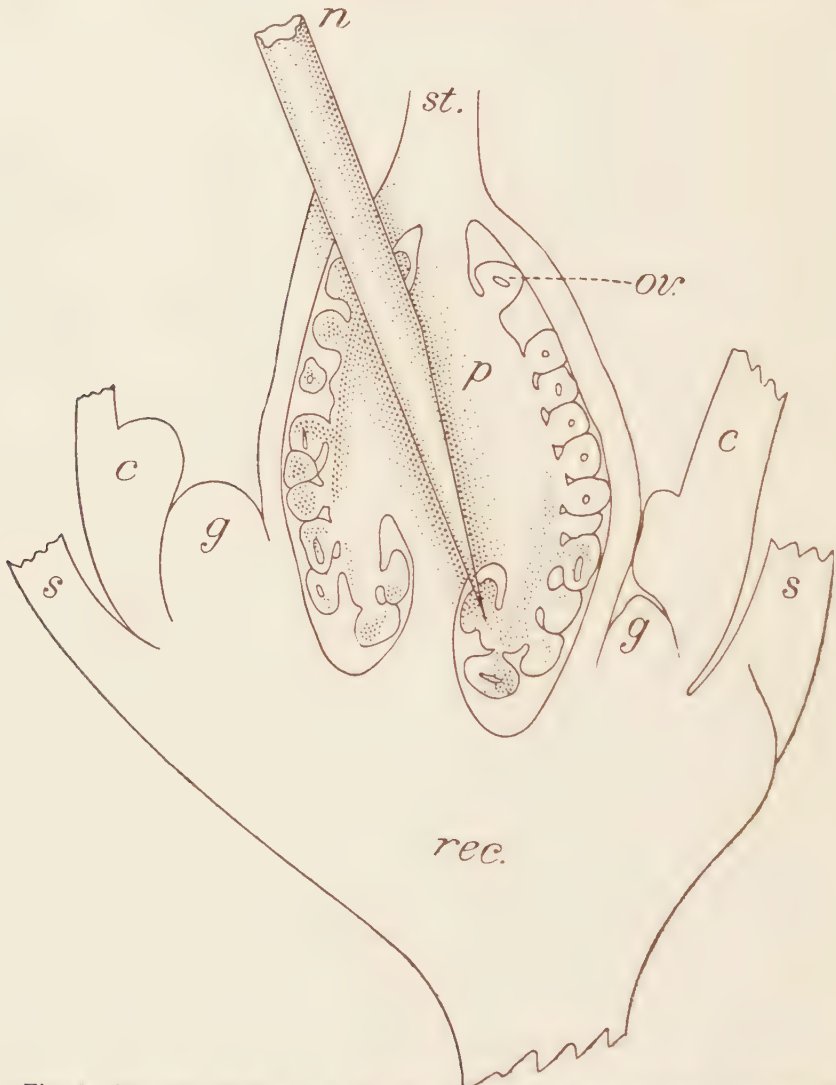


Fig. 3. Diagram of flower of *Scrophularia*, showing mechanical features of ovary treatment: *s*, sepals; *c*, corolla; *g*, nectar gland; *p*, placenta; *st*, style; *ov*, ovule; *rec*, receptacle; *p*, tip of hollow needle thrust through the ovary wall and penetrating the placenta. The stippling shows the diffusion of a solution of methylene blue introduced by the needle.—Drawn by F. E. Lloyd.

(a stable cruciate hybrid) were injected with a solution of one

part in a thousand. Fifteen to forty ovules had been touched by the color in young flowers not yet open. A much larger number had been colored in the ovaries of mature flowers. This solution was introduced into ovaries of the *Scrophularia* under examination (fig. 3). Young ovaries in this plant showed very few ovules affected, none in a few cases. Older ovaries in which fertilization had probably taken place showed as many as 15–20 colored ovules. Probably only a small proportion of the ovules affected would have survived and developed into viable seeds, so that many of the treated ovaries would have yielded nothing but normal seeds. This condition is to be taken into account by those who do not recognize the technical difficulties in the way of duplication of any particular treatment.

The recent results of Churchman and Russell¹ in securing stimulation of the growth of animal tissues with methylene blue suggest that this substance might produce some effects on the embryo-sacs of plants, and also the advantage of using a reagent the diffusion and penetration of which are visible and obvious.

It was desirable to use this dye in obtaining some knowledge of the probable action of other solutions in *Scrophularia*, so tests were made with this plant. A number of ovaries on a detached shoot in the laboratory were placed in a solution of one to a thousand at 9:30 a. m. Material was taken for examination at suitable intervals.

The placental walls and funicles were stained in part within a half hour. Two hours later the color had advanced well along the conducting tract in the funicular stalk. Five hours after treatment a notable amount of the dye had been carried clear to the embryo-sac, where it stained the nucellus and the antipodal region deeply. It is to be noted that the material was still alive and that this material if left attached to the plant would have developed some mature seeds in all probability (fig. 3).

¹ The effect of gentian violet on protozoa and on growing adult tissue. Soc. Exp. Biol. and Med., Proc. 2:124. 1914.

Professor F. E. Lloyd, of McGill University, who kindly came to my aid in this matter, now made a brief study of the intra-vitam staining in the ovules of *Scrophularia* and found that the reagent accumulated throughout the embryo-sac inclusive of the egg cell, demonstrating the possibility of the direct action of introduced solutions on the entire egg apparatus as well as upon the endosperm. The micropylar orifice was closed and was not stained in the ordinary treatments and took up only a small amount of the dye when laid separately in a solution of it. Professor Lloyd also showed me preparations in which pollen tubes deeply stained had entered the micropyle and had elongated, reaching the egg.¹ These experiments made clear the immediate possibility of reagents reaching the egg apparatus through the funicle and of the staining of the pollen tube and nucleus in the cavity of the ovary before fertilization. It is also possible that the pollen tube might be affected by reagents which had accumulated in cells through which it penetrates to the egg nucleus (fig. 4).

These facts would make it probable that treatments before pollination has taken place would affect the embryo-sac and its inclusions only, while introductions of solutions at a later stage would be likely to affect the pollen tubes and nuclei. These generalizations are to be taken to be applicable to *Scrophularia*, and to species which present similar arrangements for reproduction. The egg in ovules in which the micropyle is open might be even more readily exposed to the action of a reagent, and if the ovule is porogamous the pollen tube would also inevitably be affected, and still many other combinations may be encountered which need not be enumerated at this time.

It is of course to be understood also that not all of the ovules in any pistil are in equivalent stages of development at any given moment, and this applies also to the penetration by the pollen tubes. Pollination of *Scrophularia* takes place in the morning, and substances introduced before mid-forenoon

¹ See Lloyd, F. E. The intra-vitam absorption of methylene blue in ovules of *Scrophularia*. Report of the department of botanical research for 1914. Carnegie Inst. Washington, Yearbook 13: 77-81. 1914.

would be taken up and diffused through the tissues, especially through the funicle before the pollen tubes had reached the cavity of the ovary. Introductions timed to meet the elongat-

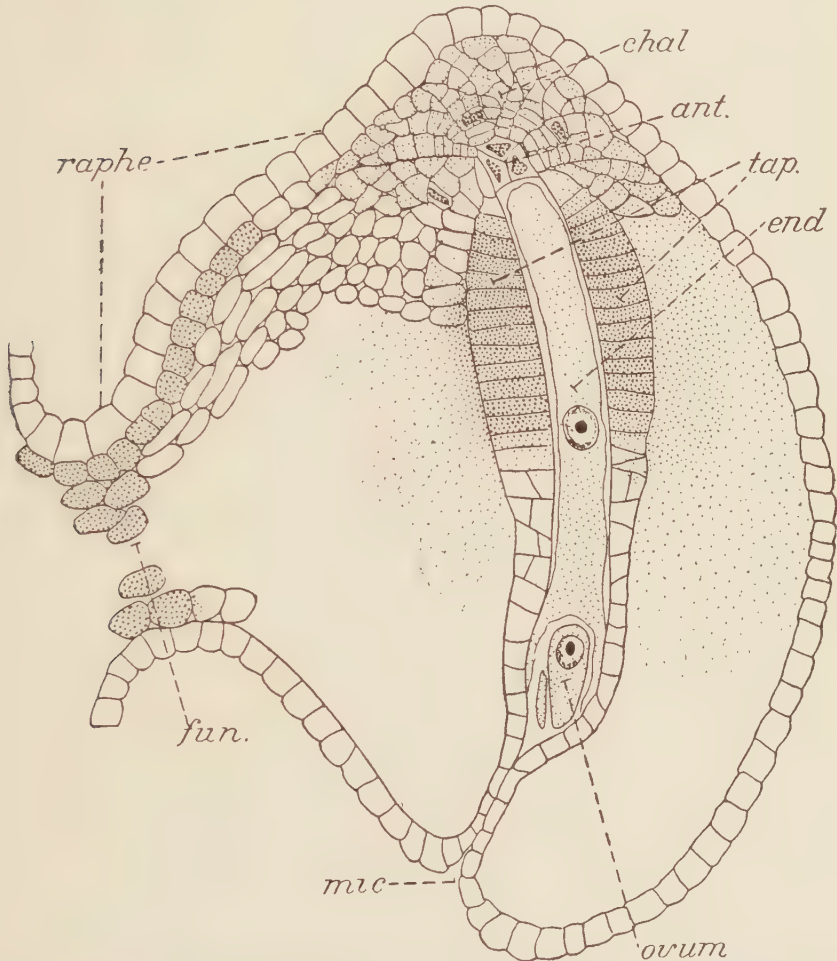


Fig. 4. Diagram of longitudinal section of ovule of *Scrophularia*: *fun.*, funicle; *chal*, chalaza; *ant.*, antipodal cells; *tap.*, tapetum; *end.*, endosperm; *mic*, micropyle. The shading shows the course of a solution of methylene blue diffusing through the funicle from the placenta (see fig. 3) and its selective fixation in the tapetum and nucellus. The solution finally reaches the ovum.

ing pollen tubes would of course be more liable to affect the pollen nuclei, and a number of lots of seeds matured in ovaries

treated at various stages of development now await germination and test.

The differences between the two surviving derivatives of *Scrophularia* described in this paper may well be due to such differential action. It is to be seen that if egg or sperm were affected singly the resultant seed into which these elements might enter would be hybrid. Even if both were acted upon, it is by no means to be taken for granted that the effects in the two would be equivalent. The F_2 of *rufida* was identical in the cultures described, while the F_2 of *albida* presented some modifications, the status of which is not yet established, as both were open pollinated in the F_1 . Very little information as to hybrids in *Scrophularia* is available. Goddijn and Goethart¹ report that *S. Neesii* Wirtg. \times *S. vernalis* L. is a unified, stable, intermediate type and that the reciprocal is of a similar character.

The behavior of the original stock, and the facts of fertilization, yield nothing suggestive of parthenogenesis, and the derivatives may be taken to be produced by a typical fertilization. No cytological examination has yet been made for the purpose of ascertaining possible differences induced in the chromosomes.

This discussion may be fittingly brought to an end by a brief reconsideration of the salient ideas which have been touched upon. The point of view taken throughout all of the work which has been described is one in which the conception of a theoretical or idealized germ-plasm has been relegated to secondary position, and attention has been concentrated upon the concrete germ-plasm of the higher plants. This physical basis of heredity is seen to present two distinct phases. In one it takes the form of a meristem or embryonic tract of highly distended cells in which auxesis and division are both rapid and the elements which are separated from it pass by differentiations into the permanent tissues of the soma. Environic agencies affect only the development of the somatic cells which are being formed from the meristem, and the ex-

¹ Ein künstlich erzeugter Bastard *Scrophularia Neesii* Wirtg. \times *S. vernalis* L. Van's Rijks Herb., Mededeel. 1913¹⁶: 1-9. 1913.

perience of these cells are not reflected back to the embryonic tract, so far as available facts may be considered. Sexually specialized reproductive elements with a reduced number of chromosomes are developed from the embryonic tracts in a late stage of the ontogeny, and these elements present a metabolic balance different from that of the meristem stage, the colloids having a greater density, and some of the energy transformations having altered velocities.

The embryonic tract or meristem of a higher plant at any given moment includes an enormous number of primitive or initial cells and of separating elements in all stages of division, growth, and differentiation toward the specialized tissues which are derived from it. The tract as a whole could therefore not react in a unified manner to any climatic or environic agency which would impinge upon the plant. Such forces, as a matter of fact, visibly affect only the manner in which the differentiation of the resting tissues takes place. The rejuvenescence of such differentiated cells might carry the effects into the organ or individual produced by the regeneration, but no test has yet been made of this matter, or of the transmission of such supposititious characters to a second sexually produced generation; neither has the proposal, that repeated or long continued exposure of the germ-plasm to any environic stimulus may result in the fixation of effects, been tested out. The continuation of introduced species in the mountain, desert, and coastal plantations of the Department of Botanical Research for the term of years during which any one person might conduct such experiments, may not be taken as an adequate test of this phase of the matter, although these cultures are carried on for the express purpose of determining what permanent changes may be induced by the tension of unusual environic complexes. So far these have been confined to alterations in sexual and asexual reproductive procedure, and to alterations in structure and aspect of the shoot, while no tests have been made upon the fixity of the changes.

Aberrant behavior of the chromosomes in certain determinative or initial cells may possibly be responsible for bud-mutations or bud-variations, and theoretically it is conceivable

that special stimuli might be applied to such cells in a manner that might bring about similar results. Practically, however, it would be enormously difficult to localize initial cells with sufficient certainty so as to give any slight chance of success.

The second stage of germ-plasm in which it is in the form of sexually specialized elements offers far more promising conditions for experimental modification of the genetic content of the species which it represents. Solutions may be introduced into the ovaries in such manner as to affect the egg bearing the entire group of qualities of the species, and furthermore the direct action of such reagents may be ascertained to some extent.

The present-day aspect of the mechanism of heredity is one which increases momentarily in complexity. The greater part of the researches in genetics during the last fifteen years has been devoted to the interaction of factors, determiners, inhibitors, or qualities in the organism. If these conceptions may be taken to be the expression of the reactions of either chemical groupings or to rest upon a physico-chemical foundation of any kind, the reagents which have been used have not been of a selective character, but would affect practically the entire colloidal mass of the protoplast in some manner and to varying extent, neutralizing or coagulating proteins, and their general tendency would be to inhibit or check energy transformations. In the case of the iodine treatments the free ions from potassium iodide or the iodic acid formed would cause a neutralizing effect, as it does not seem from the results of Czapski and Adler¹ that this element would form any compound with the proteins.

The experimenter is dealing with an actual physico-chemical complex of highly unstable compounds in which many types of energy transformation are occurring. Introduced substances may slow down or inhibit some of these, and accelerate others or start new reactions. The morphological possibilities in any given strain of plants are somewhat limited, however, and in this sense the direction of the departures is al-

¹ Beiträge zum Chemismus der Jodwirkung. *Biochem. Zeitschr.* 65:117. 1914.

ready determined. This limitation of the possibilities of morphogenesis is the chief one in any expectancy of duplication of results in successive treatments, outwardly mechanically identical.

The variables in any experimental setting are many, and the briefest consideration of the physical effects consequent upon the introduction of a foreign solution to the vicinity of the embryo-sac, reveals at once the lack of probability of exact repetitions in a mechanism so complex. The conditions are much different from those which would be presented if free floating eggs or sperms were immersed in a solution. If we are able to induce other changes in *Scrophularia* besides those shown, they will be quite as important in demonstration of the fact that germ-plasm had been modified as if they were exact repetitions of previous inductions. If previous results were exactly recalled there might be some suggestion of premutation.

It is evident that the experimenter who wishes to proceed with the greatest precision and least loss of effort will first test the genetic strictness of his living material, ascertain the rate and manner and diffusion of solutions in the ovary and ovules, the time of pollination and the rate of development of the tube in reaching the egg. Next, the structure and number of ovaries and the traumatic reactions of the entire pistil are to be taken into account. Having also traced out the simpler features of pollination and fertilization, the operator should test the effects of various reagents which may neutralize proteins, including enzymes, or act as excitators or catalyzers. Without enlarging too much upon the difficulties to be encountered in the experiments described in this paper, they may be illustrated by the fact that over fifty operations upon *Scrophularia* in July, August and September, 1914, at Carmel, California, were total failures, as the ovaries perished before reaching maturity.

Finally, many present interests in phylogeny and genetics will be concerned with the nature of the evolutionary movement which is simulated by the alterations which have been induced experimentally by the method described. Some of

these would unquestionably be designated as of a retrogressive character, such, for example, as the defection of a part of the color pattern of the corolla; others, such as the accentuated incision of the leaves and corollas and the development of the venation, as progressive alterations; while still others may not with any substantial reason be assigned to either class. With reference to taxonomic criteria, it may be said that the divergent individuals are distinguishable at sight from the parental stock, but the real test of the characters presented is not their degree or kind of departure, but their stability and permanence indicative of actual modifications of the germ-plasm.

THE RELATIONS BETWEEN SCIENTIFIC BOTANY AND PHYTOPATHOLOGY

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The ever-increasing importance of phytopathology is the result of the steady development of agriculture, forestry, and horticulture. In this way phytopathology has become a part of each of these sciences.

In former times well-known botanists, such as Gleditsch, Martius, Caspary, de Bary, and Sachs did not estimate themselves too highly to concern themselves at times with phytopathological problems. In modern times, however, it is not often that a university professor of botany occupies himself with such problems. This is due partially to the specialization which has become a necessity in modern science. Above all, however, this is due to a peculiar conception which looks upon the applied branches of applied natural science as something inferior to the pure natural sciences. It must, however, be said that we find exceptions even here, if we think of such scientists as Brefeld and De Vries.

Agriculture has within a short time presented many problems to phytopathology, and of these the principal ones have been those of disease control. These problems were often solved in a hasty way, which, I must admit, lacked scientific thoroughness. But even in the solution of these problems many interesting facts were brought to light. But with the progress in working out these questions it became more and more evident that many of these problems could not be ultimately solved unless investigated in a thoroughly scientific manner.

In criticising the plant pathologists it should not be forgotten that most of them are for the greater part autodidacts. Until recent times there were no places where scientific phytopathology was taught. In Germany it was only the

University of Munich, in which von Tubeuf has been and is still teaching the subject. In Austria, Hecke has been giving lectures for some years. In the United States there has been much progress in this line, due, no doubt, to the fact that plant diseases are of greater importance here than in any other country. As the number of chairs in phytopathology in our institutions of learning increases, however, the relation between scientific botany and phytopathology will become more and more intimate.

Among the factors which favor unusual ravages by vegetable and animal parasites, I wish to mention the rapid development of agriculture by way of growing the same varieties or races over vast areas, the great fertility of the previously uncultivated soils, which often induced people to crop the soil and neglect rotation, and lastly the favorable climatic conditions, which not only favor the cultural plants but also their parasites.

One of the oldest problems of phytopathology is the smut-problem. Since ancient times smuts have been among the most important plagues of our cereals, and long before we knew the cause of these diseases people tried to control them. But rational measures of control could not be developed before the cause of the disease was known. Julius Kühn succeeded in clearing up the life-history of the stinking smut. This was the first distinct step in advance, but here, unfortunately, progress ceased for some time, principally because of the lack of knowledge concerning the taxonomy of the smut-fungi. All loose smuts of oats, wheat, barley, and the close smuts of oats and barley were united under the single species *Ustilago carbo*. This prevented the investigations of the biology of the smuts, and it was not until the fact was demonstrated that various species of smuts were concerned that the way was opened for the proper investigation of the biology and subsequently also of the control of the parasite.

The development of our knowledge of the smuts was due to the biological facts demonstrated by Brefeld and Hecke. They discovered that infection takes place through the

flowers. This fact pointed out the way of control. The problem was to kill one organism, the smut-fungus, within another organism, the grain seed, without doing damage to the latter. Jensen by his empirical work had demonstrated that such a procedure was possible. The correct method of control, however, could not be worked out because of the lack of knowledge concerning the fundamental scientific facts involved. In order to establish such a firm basis, I, together with my assistant, Riehm, studied the resistance of the smut-fungi to external conditions, primarily to the effects of temperature. When the mycelium was grown in water and other substrata we demonstrated the fact that the thicker-celled mycelium as well as the spores are more resistant to external influences than is the vigorously growing mycelium. However, not only the smut but also the grain is more resistant in the resting period than when germinating. Therefore, we tried to bring the infected grain seed under conditions which cause the fungus to grow and which at the same time do not allow the seed to germinate. We succeeded in doing this by allowing the seeds to remain for about four hours in water at 25-30°C. If one then subjects the seeds to a temperature at which the mycelium is killed but which does not yet induce germination in the grain, it is possible to kill the mycelium in the seed without injuring the latter.

In these investigations the key to the so-called hot water and hot air treatment was found, and it was then only a technical problem to build apparatus with which the desired results could with certainty be realized. For our conditions in Germany this latter problem has also been solved. We have constructed several pieces of apparatus of this sort, and the treatment of grain against loose smut has been introduced on many farms.

But the smut-problem has not been solved for all cases. This is especially true in the case of the stinking smut in the United States. This disease is of the greatest importance in the wheat districts of Idaho. In Germany *Tilletia Tritici* is spread by the seeds and is controlled by seed disinfection. In Idaho it occurs so generally in the soil that disinfection is

of no avail. Losses of 25 per cent of the crop are not uncommon. The solution of this problem seems possible only by the breeding of disease-resistant varieties. It is certain that smut-resistant races of wheat exist. The problem is to find these varieties and, in case they are not sufficiently productive, to cross them with other varieties until races which combine the desired characteristics are obtained. In the districts where smut occurs every year it is possible to find these races in an empirical way. But in general it is my opinion that all work of selecting and breeding should be prosecuted along fundamental scientific lines.

It is therefore first of all necessary to determine to what characters the plant owes its disease-resistant qualities. When this has been accomplished it is next necessary to determine to what extent the characters are heritable, that is to say, whether they appear in crosses as dominant or recessive. The great advantage of this method lies in the fact that it makes it possible to recognize resistant races (by the presence of the specific characters to which resistance is due) without infection experiments, which are uncertain owing to the influence of external and unknown conditions.

I have shown to you by this example that in the solution of a single phytopathological problem such diverse branches of botany as taxonomy, biology of the flower, fungus-biology, and inheritance are involved. The following examples will show that in addition other branches of botany are of importance in phytopathology.

In exact phytopathological investigations it is a primary factor that one know the host plants and the parasites in detail. This information must be based upon thorough systematic knowledge. This seems to be very easy in cultivated plants, the species of which are generally well distinguished. Some cases, however, are more complicated. When we want to make studies of cereal rusts, it is not sufficient to know the races of cereals by their agricultural names. We must know to what botanical species they belong; our cultivated wheats, for instance, comprise species of different susceptibilities.

Much more difficult are the systematic relations of the fungi. Many experiments and publications are valueless because the identity of the fungus was not made sure of in every single case. These difficulties are greater in case the fungi in question belong to the *Fungi Imperfecti*, where very often only the name of the genus has been determined, while the species name was simply made from the name of the host. Moreover, the descriptions of these imperfect fungi are often so insufficient that it is impossible to identify the fungi afterwards, especially when they occur on other plants or on a different or unrecognizable substratum. Within a genus that is rich in species there have sometimes been erected so many species that there is no possibility of identification. We find an instance of this in the genus *Fusarium*. Several hundreds of species have been described; which of these are identical has not yet been made clear, and in many cases this may never be possible. We cannot always solve the problem by making use of the exsiccata of the author of the species. Moreover, on one species of host several species of *Fusarium* may be harbored, and the author has often considered them identical. It is further often impossible to find what fungus was the type of the author's description. In such a case the only alternative is a thorough reworking of the taxonomy. How extensive a work this may often involve is instanced by the genus *Fusarium*. To establish the fundamental facts regarding the taxonomy within this genus required four years of work on my part as well as on the part of my assistant, Dr. Wollenweber, who devoted all of his time to the subject.

Even after the establishment of these fundamental facts, only a very small part of the species had been determined, and for another two years Wollenweber has been working up the remaining species. I wish only to point out in addition that there exist more genera of this type: *Botrytis*, *Gloeosporium*, and *Alternaria* and its relatives.

Modern taxonomy of fungi cannot limit itself to the morphology of the species casually collected. It must have the help of pure cultures on various media, for in artificial culture additional differences show themselves. These differ-

ences are not only biological, such as color formation and changes in the culture media, but also morphological, such as the form of the "Fuszellen" or basal cells of species of *Fusarium*, and even gross, as, for instance, differences in form of colonies, etc.

In the first place, artificial culture is of enormous value as it furnishes the proof of the presence or absence of a relation between different forms of fungi. This knowledge not only gives us a better insight into the development of the organism, but also gives us most important information as to the methods of control.

In the identification of bacteria cultural methods are absolutely necessary as these organisms cannot be determined otherwise. The determination of the host and its enemies is not only desirable on the ground given above, but also because it gives us opportunity for ecological observations. A disease occurs only when conditions are favorable to its development, and these conditions are often pointed out by the composition of the flora of the locality, of which my studies upon the dying-out of alder trees in Germany give you a clear proof. In different localities these trees are killed by a fungus, *Valsa oxystoma*. The fungus grows into the wood through wounds, especially where branches or twigs are broken off, and kills out parts of the cambium and the bark. The parts into which it does not penetrate remain alive. There was no doubt about the fungus being the cause of the disease, but there were groups of trees which, though the fungus was present, were not quite killed out, the damage done in these localities being much smaller. I hit upon the correct explanation of this condition through a study of the special character of the flora under the trees. It was a typical flora of pastures, in which occurred specimens of *Iris pseudacorus* and retreating areas of *Carex paniculata*. These two plants are typical inhabitants of the peats, or water borders. It was clear that the locality had been formerly of a peaty character. I could determine that recently the water level had been lowered for the formation of artificial meadows. Without a knowledge of the flora this relation would never have been found, as these meadows

were situated behind a chain of hills. The depth of the ditches had changed the water level and prepared the right conditions for an attack of *Valsa oxystoma*.

In another paper I have shown the importance of the work of E. Münch.¹ This work is a model as to the manner in which investigations of plant diseases upon a scientific basis should be prosecuted. And, therefore, I wish to come back in a more detailed way to the work of Münch. The fungous diseases of our trees belong, in general, to the most important diseases, and we yearly lose millions on their account. But we did not know the factors upon which the appearance of such diseases rested until these were demonstrated by the work of Münch. It was known that many fungi attack woody plants under definite conditions. Sometimes closely related species of one genus of hosts behave differently and sometimes only definite tissues are attacked. Lastly these relations vary in different years or seasons in different localities. The difficulty has been that the cause of this variability was sought in the different soil conditions which might have an influence on the constitution of the tissues of the host, in external injuries—such as sunburn or frost, and in the period of development of the fungus. These factors, however, are not of fundamental importance in the question of the production or suppression of a fungous attack.

Münch has proved through numerous experiments that the content of air in the tissues is the determining factor. The greater part of the wood-decaying fungi have a large air requirement and are able to grow only when a maximum of air is furnished. In the first place the content of air is dependent on the quantity of water, and the occurrence of this large class of plant diseases depends upon the water supply. Similarly, the quantity of solid substance may be of influence. Specimens with narrow annual rings are more resistant than those with broad ones, because there is less room for air in the former. The different annual rings of the same wood

¹Untersuchungen über Immunität und Krankheitsempfänglichkeit der Holzpflanzen. Naturwiss. Zeitschr. f. Forst- u. Landw. 7: 54-75, 87-114, 129-160. 1909.

may be attacked differently, which is supported by the evidence of many observers. Not infrequently do we find tree trunks in which only some annual rings have been infected, or in which the same ring is diseased on one side and healthy on the other. The decayed rings are always the broad ones. The same varieties have a different air content in different localities. In the neighborhood of water sprouts or vigorous branches, the tissues are rich in water and poor in air, and infections very often do not penetrate into such regions. We know now that poorly fed and crippled specimens are likely to be attacked; on the other hand, it seems clear that fruit trees which are richly fed with nitrogen are very susceptible to canker. An abundance of nitrogen induces the development of a very loose tissue, which during drought is more subject to diseases than a firm tissue. We recognize the periodicity in the occurrence of many plant diseases, for we know the fluctuations in the water content of a tree. The air content of the healthy bark of beeches in winter-rest is 19-20 per cent, and diminishes at the time of budding to 11 per cent, rising afterwards. This is correlated with the fact that the canker, which in Europe is caused by *Nectria ditissima*, does its damage from autumn until spring, while this damage ceases during the vegetative period. This was pointed out by Aderhold, who, however, failed to recognize the cause.

If once we know the absolute percentage of air necessary for fungous growth in the different kinds of wood, we may decide through direct investigation whether in certain localities the danger of infection is large or small. We may test the different varieties and try to avoid the danger. By this method the control is not directed against the fungus, but against the conditions which make its growth possible. In other words, we use instead of direct control, measures which prevent the outbreak of epidemic diseases.

You see by this example what an exactly planned scientific investigation may do, and you can recognize the application of these facts to the American conditions. In the irrigated districts the fruit trees have but few die-back diseases due

to species of *Valsa* and other fungi. When, however, such diseases occur, you will find the cause in defective irrigation methods, which may be remedied by changing the irrigation system. It is of the greatest importance that the land be irrigated at the time the trees contain less water and plenty of air, and that the next irrigations be made in time to prevent an excessive decrease of the water in the tissues.

Not all fungi, however, are dependent upon the air contained in the wood. This is, for instance, the case with *Armillaria mellea*, where the rhizomorphs bring a sufficient quantity of air into the inner tissues. Whoever has cultivated the fungus artificially knows that after a short time rhizomorphs are formed which grow deep into the medium. But the rhizomorphs are not formed on all kinds of trees and it may be possible that the fungus in these cases depends on the air already in the wood.

Another question of great importance for American conditions is the question whether the growth of bacteria, principally of *Bacillus amylovorus*, is dependent upon the air content of the host or not. These experiments must be supported by thorough physiological investigations. That manner of control which seeks to remove the bacteria by cutting out the branches does not guarantee success for the future. I have been convinced of this in my trip through the United States, where I visited districts in which this control measure was thoroughly carried out.

It may be possible that not only trees, but also herbaceous plants, show relations between fungous growth and air content. I think it must be so for the organisms which cause the wilt diseases and the rhizoctonia disease of the potato, both of which have a high air requirement. On media poor in air these fungi grow only on the surface and absorb very eagerly the oxygen of hydrogen peroxide. The growth of *Rhizoctonia* in the well-aërated peat soil of the Stockton Delta and the forest soil of Germany is more marked in the dry years than in the years when the plants get a sufficient supply of water. In the United States these diseases are wide-spread, principally through the irrigated lands. In my trip I came to the

conclusion that these diseases are not to be controlled by fighting the fungi, but by influencing the potato plant. Though caused by a fungus, the production of the conditions favorable to the progress of the disease is attributable to irrigation. In many cases the root system was poorly developed, the different kinds of irrigation showing an influence upon the growth of the underground parts of the plants. We know very little of the conditions of growth of the potato in spite of a few publications on this subject by Müller-Thurgau, De Vries, and Vöchting. Moreover, we know nothing about transpiration and water requirements in these plants or about their ability to form roots, or the factors that influence these processes. It is, therefore, very important that Shantz, of the Department of Agriculture, has actually undertaken the investigation of these problems. Others must follow him as soon as possible to solve these questions for the irrigated lands.

The chemical-physiological side of the phytopathological questions also needs more attention, as has been pointed out recently by me and others in work upon the freezing problem. For a true judgment of the resistance to frost, in the case of cereal diseases, Gossner has apparently found the right way. The earlier stated fact that the cells of small pieces of tissue floating on a sugar solution are less quickly killed by frost than when floating in water, made it probable that the young plant is protected by sugar against frost injury. The investigation of the winter and summer rye shows that the sugar content of the former is several per cent greater than of the latter. The same is the case for frost-susceptible races of wheat. We may thus find out the relative frost resistance of closely related races of plants by determining the sugar content.

But other phases of chemistry are of importance in phytopathological investigations, as, for instance, the chemistry of colloids, which, as Ruhland showed in his work, is of great value. The microchemical reactions are also of great importance. We know today that cork formation in the potato is a protection against bacterial invasion. I could show by using the reaction of Tisson that the deposition of

cork in the cell walls near the places of infection occurs earlier than the formation of cork plates.

Of special interest is the physiology of inheritance. In this lecture I wish merely to emphasize that the inheritance of the unit characters and their behavior in the next generation is one of the fundamentals of breeding resistant races.

Finally, I must speak of anatomy. The necessity of the examination of series of sections oblige the pathologist to make use of the latest discoveries in histology. It is by way of anatomy that we shall approach the problem of leaf-roll of the potato. Onemjer has shown that the sieve tubes, which have the function of providing the plant with albumen, are destroyed in the leaf-rolling plants, similar symptoms occurring in plants which suffer from other diseases only when the plants are nearly dead. In leaf-rolling plants, however, we find these changes from the very beginning, and we may use them in diagnosis. Anatomy, likewise, points out relations between external disease symptoms and inner changes of structure. For instance, the three inner diseases of the potato, leaf-roll, wilt, and bacterial ring disease, have distinguishable anatomical characters; the leaf-roll is a disease of the phloem; wilt, of the secondary wood vessels; and bacterial ring, of the spiral vessels. A thorough anatomical knowledge is of primary importance in all investigations concerning the inner structure of healthy and diseased plants, the formation of excretions and tyloses, and the different ways of recovery.

I hope that it has been possible for me to show you that phytopathology has many fundamental relations to scientific botany, and that it further presents many important problems for scientific investigation which deserve attention from the botanical departments of universities.

Should I have succeeded hereby in winning new friends to phytopathology in this sense it would be a source of genuine satisfaction and pleasure to me.

THE LAW OF TEMPERATURE CONNECTED WITH THE DISTRIBUTION OF THE MARINE ALGAE

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What I have to bring before you is simply a preliminary consideration of the general subject of the geographical distribution of the marine algae together with some inquiry into the conditions immediately affecting such distribution and as possibly effecting a segregation into the larger units. In accordance with such an intention, I have started a tabulation of all the marine species and varieties, which is far from being completed as yet, but which has, however, reached a stage at which certain general statements may be made as to probable results.

The geographical distribution of the marine algae has been treated of in various ways and in many papers. It is more or less customary to make a comparison between a particular flora and other more or less corresponding floras in comparative tables, percentages of common and endemic species, etc. Certain speculations, based on such data, as to the origin of certain algal floras have also been indulged in. The result is that we have certain geographical areas fairly well marked out and certain others more or less indistinctly outlined or surmised. Certain ecologic classifications have been proposed, particularly as to zonal occurrence in varying depth, influence of varying degrees of salinity, character of the substratum, influence of surge, quiet waters, etc. Very little attention, however, has been paid to general factors controlling distribution over larger areas. We speak broadly of tropical species, or of arctic or antarctic species, of temperate species, etc., but no attempt has been made to survey the distribution of marine algae in general throughout the oceans and seas of the world and to attempt to determine the limiting factors segregating one large area from another. An attempt to determine how far our present knowledge of

species and their distribution may further such an inquiry is the object of the present paper.

Among the more general discussions, there are to be mentioned first those connected with the geographical distribution in the Arctic Ocean. Kjellman's extensive and fundamental paper 'Algae of the Arctic Sea' ('83) led the way and placed at the disposal of future students a very considerable amount of data and brought forward certain fundamental points of view as to a division of the arctic marine flora into provinces, as well as a consideration of the conditions underlying this division. This work was the result of the working over of very considerable collections of the various Swedish expeditions into the Arctic Ocean and a careful examination of all other existing data.

Later, Rosenvinge ('93, '98, '98^a, '98^b) published a series of papers dealing with the marine flora of Greenland, and Jónsson ('03, '03^a, '04, '12) has also published on the same subject as well as on the algae of Iceland and Jan Mayen.

Finally, somewhat over twenty years after Kjellman's paper, Simmons ('05) surveyed the whole matter, revised all tabulations of the Arctic flora and brought forward further views together with a full discussion of all literature bearing upon the subject.

In these various papers and others not referred to specifically, the North Polar Sea is defined and delimited from the Northern Atlantic and Northern Pacific Oceans. The conditions under which marine algae occur in the Polar regions as well as the differences between the conditions of the various portions of its waters are also determined and discussed.

The North Atlantic has also been treated of, but more floristically than as to uniformity, or differences, of physical conditions affecting the flora. A considerable part of the discussion regarding the North Atlantic Ocean has centered about the Faeröes. Simmons ('97), Börgesen ('02, '05), Por-sild and Simmons ('04), and Börgesen and Jónsson ('05), have discussed the marine flora of these islands together with its relation to other North Atlantic floras and ocean currents. Reinke ('89), Svedelius ('01), and Kylin ('06, '07),

have considered the algal flora of the Baltic Sea and its relation to that of the North Atlantic from points of view both floristic and as to physical conditions. Harvey ('58), Farrow ('81), and Collins ('00), have dealt similarly with the algal flora of the northeastern coast of North America, and Börgesen and Jónsson ('05) have made an extended floristic comparison between the floras of the North Atlantic and those of the polar or arctic seas.

For the antarctic and subantarctic regions, the work even of floristic comparison is still hampered by incomplete knowledge. The foundations were laid by Hooker ('45) in the 'Cryptogamia Antarctica' in which there are scattered notes on distribution. Skottsberg ('06) published his 'Observations on the Vegetation of the Antarctic Sea' and later ('07) the first part of his antarctic and subantarctic work. The latter has only floristic details with notes on distribution. Gain ('12) has given a detailed discussion of the distribution of the marine algae thus far credited to either the antarctic or the subantarctic regions of the western hemisphere. Murray and Barton ('95) have given a comparison between the arctic and antarctic marine floras, and Mme. Lemoine ('12) has made a similar comparison limiting it, however, to the species of crustaceous *Corallinaceae*.

The distribution of marine algae in the warmer portions of the oceans, Atlantic, Pacific, and Indian, has not been so much considered as that of the colder portions, although very considerable floristic work has been done. Murray ('93) published a comparison of the marine floras of the warm Atlantic, Indian Ocean, and the Cape of Good Hope. Yendo ('02) has made definite statements about the distribution on the coasts of Japan. Saunders ('01) and Setchell and Gardner ('03) have dealt with the northwest coast of North America, and Schmitz ('96) and Schroeder ('12) have called attention to the relations between the marine flora of East Africa and those of the East Indies and of the central Pacific Ocean.

Various papers and floras have considered distribution, such as bathymetric zonal distribution or according to varying substratum, salinity, etc., within limited regions, prov-

inces, or districts, but no general paper has as yet appeared dealing with the distribution over the oceans in general or any definite suggestions as to the factors concerned.

The nearest approach to an attempt to account for the general facts of distribution is my own attempt (cf. Setchell, '93) to explain the main facts of the geographical distribution of the *Laminariaceae*. The plants of this family are rather inhabitants of the colder than of the warmer waters, proceeding, as it were, from the poles towards the equator, but lacking in strictly tropical waters. It was found that the *Laminariaceae* flora changed its facies with every increase or decrease of 5°C. of summer temperature, thus forming latitudinal zones controlled by temperature relations. This idea was extended to explain the demarcations of the floras of the west coast of North America by Gardner and myself (cf. Setchell and Gardner, '03) with apparent adequate reason.

In attempting to discuss the more general facts of distribution we first necessarily consider the various marine floras and their subdivisions. While the term flora has been used in all sorts of senses, both wider and narrower, to include any aggregation of plants of any region under discussion, whether larger or smaller, it generally carries a certain idea of uniformity of composition with it when used in connection with the floristics of distribution. This uniformity may, however, be only as regards region. It is desirable, here, to use the word for the aggregation of species of marine algae found in a certain region, province, or district, having a certain fairly considerable percentage of species in common throughout its extent, even of the more extended region.

The world's surface, whether land or water, is usually divided into zones of temperature, these in turn into regions, the regions into provinces, and the provinces into districts. For marine floras, the districts must be still further divided into formations, and these in turn into bathymetric or littoral belts. The bathymetric belts, in their turn, show different algal associations.

Considerable work has been done in the description of various floristic associations occurring in various depth belts and of various formations, and the special ecological relationships have been discussed and made reasonably plain. My intention, however, is to discuss the broader distribution and segregation of floras, particularly as to regions and perhaps provinces and to attempt to determine the factor, or factors, governing these.

In attempting to mark out the various floristic regions and their provinces, we are met with certain difficulties. The flora of the Arctic or Boreal region is fairly definite and has been the most carefully studied and tabulated. The provinces of the Arctic region are the Asiatic, the American, that of West Greenland, and the extended province of Spitzbergen (cf. Simmons, '05). The North Atlantic Ocean as distinguished from the Arctic has five regions, viz., those of Northwestern Europe, Southwestern Europe, and the Mediterraneo-Northwest African region on the east and Northeastern North America and Middle eastern North America on the west. The Antarctic or Austral region possesses a fairly consistent flora and is not so readily divided into provinces, but the Antarctic-Magellanic province may be contrasted with the Indo-Pacific province. The South Atlantic Ocean has a flora as yet little understood, but, for the present at least, may be considered to have the regions of Southwest Africa and Southeast South America. The Northern Pacific has Bering Sea probably representing a province of the Arctic or Boreal region. Otherwise it is divided into five regions, viz., those of Northwest North America, Middle West North America, and Southwest North America on the east and the Ochotsk-Yezo region and that of East and West Honshu (or Nippon) on the west shores. The South Pacific Ocean has five regions, viz., those of Southwest South America, Middle West South America on the east and those of New Zealand and South and Southeast Australia on the west coasts. The southern portion of the Indian Ocean has two regions, viz., that of Southwest Australia and the South Africa or Cape region. The tropical waters may probably be divided into two regions, viz., the

Tropical Atlantic and the Indo-Pacific regions with their proper subdivision into provinces. Concerning these various regions, it may be said that some seem to possess very distinct and characteristic species content while others are more or less related to one another. However, it is expected that there will be a possibility of discussing this segregation at another time in more extended fashion.

Of particular interest and importance in connection with the marking off of floristic regions, are the points or areas of demarcation. Some of these are well established while others may be only more or less accurately surmised. One of these much referred to in the literature (cf. Harvey, '58; Farlow, '81; etc.) is Cape Cod on the eastern coast of Massachusetts which divides so clearly and so accurately the flora of northern New England from that of southern New England. Cadiz in Spain appears to be another point of demarcation, or possibly indication of an area, where the flora of the Southwestern European region stops, or mingles with that of the Mediterranean-Northwest African region. At Clare Island on the west coast of Ireland (Cotton, '12, p. 160) the flora "resembles that of the southwest of England," but it has elements also of a distinctly northern character. It is probably in or near a demarcation area. Similarly southern Norway and the west coast of Sweden (Kjellman, '02, '06; Svedelius, '01; Kylin, '06, '07) have a mixed flora and are in a transition region.

In Japan Cape Inuboi on the east coast of Honshu (cf. Yendo, '02, p. 181) is a demarcation point and the Strait of Sangar (cf. Yendo, '02, p. 182) is also a region of demarcation or transition. On the opposite side of the Pacific Ocean, along the western coast of North America, Cape Flattery or just south of it, Point Conception, and the region about the mouth of the Gulf of California are demarcation points or indicate transition areas (cf. Setchell, '93, p. 370; Saunders, '01, p. 393; Setchell & Gardner, '03, p. 170). In the southern hemisphere the marine flora of the Cape Region is definitely delimited both to the southwest and to the northeast and in

Australia the marine flora of the southeastern region is definitely set off from that of the southwestern region.

These various points and regions will doubtless become more definite and more of them will become established as careful investigations of the floras are made. They undoubtedly indicate that thereabouts are changes in the conditions regulating the separation of the general flora into its larger divisions and are of great importance in any inquiry as to the general factors affecting the distribution of marine algae.

Along with the mapping out of floras into regions, provinces, etc., it seems best to consider, next, the factors which seem to regulate the distribution. These have been considered by Kjellman ('83) and by others, and are summed up by Oltmanns ('05). Particularly is it desirable to consider which may be chiefly responsible for the limiting of the species within the regions or provinces.

The substratum exercises an important influence on the attached flora or benthos and that is particularly the part of the marine flora I intend to limit this paper to, since the plankton brings in certain particular factors having to do with its floating habits. Of course, benthos can only exist on its proper firmer substratum and different species differ in the nature of this. However, it is sufficiently evident that the character of the substratum limits species only locally and can by no means be considered as a factor in controlling floral regions or even floral provinces.

The motion of the water is a limiting factor in distribution, some algae preferring quiet water, some flowing, some surge, etc., but this factor, too, is clearly a local and not a general one in the distribution of the marine algal benthos.

The specific gravity of sea-water varies and with it, of course, its salt content. This variation, so far as marine algae are concerned, varies from water only slightly brackish to that (in case of exposed and shallow tide pools) of an almost concentrated solution. There is a latitudinal zonal difference here also, but it is not so great as may be found in localities at no considerable distance from one another. It

certainly seems impossible that this can be a general factor. Its local effect, however, may be very considerable.

Light varies from the equator, where it is most intense, to the poles where it is least. It very decidedly limits the distribution as to depth. Marine algae of the benthos need light and are, therefore, limited to the neritic portion of the photic zone as to their general distribution. Outside of this general limitation, however, it does not appear that the varying intensity of light can be considered as a prime factor in limiting floral regions and floral provinces, i.e., not alone.

Varying temperature, however, does act directly upon algae to limit their distribution, both locally and generally. It can easily be recognized to be the one most important factor in controlling the distribution of benthos over wide areas as well as, at times, in smaller districts or spots. We recognize that, in general, the species of the frigid zones, of the temperate zones, and of the tropical zones are sufficiently different to give an entirely different facies to each. Yet, in considering general regions, we find that they are not marked out by the same parallels as are used to mark these zones geographically. These geographical zones, however, are established more particularly as regards direction of the sun's rays and the temperature of the air rather than that of the water.

The waters concerned with the life and persistence of the algae, even of the benthos, are, relatively speaking, the surface waters, since algae seldom grow lower than at a depth of 100 meters and for the most part cease at 20-30 (or at times 40) meters. The normal decrease in temperature at such depths is slight even in temperate waters, although, at times, sufficient to account for special sporadic anomalous distribution. The range in temperature under which algae, in general, may carry on their full course of vegetative and growth activities is from $-2^{\circ}\text{C}.$ up to the neighborhood of $90^{\circ}\text{C}.$, but that for marine algae is only from $-2^{\circ}\text{C}.$ up to $30^{\circ}\text{C}.$ (or possibly $32^{\circ}\text{C}.$), this being the extent of ranges for all surface waters of the ocean.

A comparison between charts in which the isotherms for surface temperature of the water of the oceans are laid off

shows a definite correspondence between certain of these lines and the boundaries of different marine floral regions as previously laid out and indicated in this paper.

From the point of view of the distribution of the marine benthos, so far as algae are concerned, it is found by practice to be satisfactory to divide the surface waters of the ocean into nine zones, as follows: Upper Boreal, Lower Boreal, North Temperate, North Subtropical, Tropical, South Subtropical, South Temperate, Lower Austral, and Upper Austral. The limiting isotherms of surface temperature chosen are those of the summer month or maxima, viz., the isotheres, which are those of February (or possibly March) for the southern hemisphere and those of August (or possibly September) for the northern hemisphere. These lines are laid down with approximate accuracy in the charts of the atlases of the different oceans published by the "Deutsche Seewarte" of Hamburg ('92, '96, '02). These isotherms are more accurate and explicit for the open ocean than for the neritic zone where the algal benthos occurs, but, with certain allowances, the zones as indicated are sufficiently accurate.

Each of the zones I have proposed covers 5°C. range of surface temperature with the exception of the Upper Boreal and the Upper Austral, each of which includes a range of 10°C. or slightly over. The zones, then, more or less arbitrarily adopted, are the Upper Boreal and Upper Austral, between the isotheres of 0°C. (or even -2°C.) to 10°C., Lower Boreal and Lower Austral between the isotheres of 10°C. and 15°C., North Temperate and South Temperate between the isotheres of 15°C. and 20°C., North Subtropical and South Subtropical between the isotheres of 20°C. and 25°C., and the Tropical between 25°C. and 30°C. (or above).

These 5°C. zones are thus laid out according to the 5° isotheres, because on inspection these isotheres approach most closely or touch the shores at the division points of floras and principal floral provinces. They have been determined empirically, and indicate, as it seems from experience in working with them, that they coincide with floral boundaries the oceans over more exactly than do any of the

winter isotherms or isocrymes, or any of those in the intermediate seasons.

For example the isotherm of 20°C . passes somewhat south of Cape Cod to the eastern end of Long Island, but the shallow and more or less protected waters of Long Island Sound, Narragansett Bay, Buzzard's Bay and Vineyard Sound carry a higher temperature eastward even to the Cape Cod region. At exposed points, however, the somewhat colder waters of the ocean outside exist and exercise their influence at exposed points or in deeper waters.

Again at Cadiz, the isotherm of 20°C . abruptly curves up to the coast. At Cape Inuboi, Japan, the isotherm of 25°C . touches land and at the Strait of Sangar, that of 20°C . The Cape Region of South Africa is included between the isotherms of 20°C . and 25°C . Similar relations hold good on the coast of Ireland, for the 15°C . isotherm comes in just north of Clare Island at about Annagh Head. On the south coast of Australia, the isotherm of 20°C . touches the east coast just above Cape Howe and the south coast about Cape Arid, thus leaving the southeastern coast below 20°C . of average summer temperature and the southwestern coast above it. Although the western coast of North America has its temperature relations very much disturbed, as I shall indicate later, yet there is a fairly definite relationship to the isotherms of 10°C ., 15°C ., 20°C ., and 25°C . The arctic or boreal floristic region has a definite southern boundary in the 10°C . isotherm and the subarctic in that of 15°C ., while those of the North Atlantic are bounded to the south by that of 25°C . The strictly tropical species are found almost entirely between the isotherms of 25°C . and 30°C . (or 32°C .). It is expected that a later paper will deal more definitely and in more detail with the reasons for selecting the isotherms as bounding lines for the temperature zones.

Two seeming disturbances of those zonal areas may be noted in passing; one is that the polar zones (Upper Boreal and Upper Austral) are for 10°C . interval rather than 5°C . This is in accordance with what is known of the distribution of the marine flora in the higher Arctic and the higher Ant-

arctic regions, where there seems to be no useful purpose served in segregation by assuming two zones rather than one. The second disturbance of zonal areas is through the occurrence of local areas, of greater or less extent, of water of a higher or lower temperature than is normal for the general zone. Colder waters occurring among warmer waters are found along the west coasts of North and of South America, of northwestern and southwestern Africa, and of northeastern Africa. These are due to currents or to upwellings of cold water. Their existence is well substantiated but their cause is still a matter of discussion among oceanographers. When warm waters exist among colder waters, they occur as "spots" or small areas where the higher temperature is due to comparatively local factors apart from general oceanographic conditions. Such disturbances as upwellings and spots may bring about a puzzling discontinuity in the distribution, very puzzling, indeed, until the immediate cause is discovered.

Another matter causing seeming disturbance of the limits of temperature zones proposed is the seasonal variation of the temperature of the surface waters. This is variable, but in general may be considered to hold true as follows: The seasonal surface temperature variation as platted for 2° squares is least in the Upper Boreal, Upper Austral and Tropical zones, where it is not over 5°C. in range; is greatest in the Temperate zones where it averages nearly 15°C. and may be as great as 27 or 28°C., and is medium in the Subtropical zones and in the Lower Boreal and Lower Austral zones where it approximates 10°C.

These, then, are the principal features of temperature distribution with which we may be concerned.

In connection with the empirical establishing of the temperature zones previously outlined, I have attempted to arrange each and every species of marine algal benthos thus far described in the zone or zones to which it has been accredited. The work is not as yet by any means completed, but a general view has been obtained for the *Rhodophyceae*, *Phaeophyceae*, *Chlorophyceae*, and *Myxophyceae*, and the greater part of the

Rhodophyceae have been worked out in fair detail, although no percentages of absolute accuracy can be given at present. The general results are as follows:

(1) The greater part of the species are known from one zone of temperature.

(2) A considerable number of species are known from two zones of temperature.

(3) A comparatively small number are credited to three zones of temperature.

(4) Species credited as occurring in four or five zones of unlike temperature are extremely few and almost always doubtfully so accredited.

(5) There is a change of facies of the flora in each successive zone, i.e., with every increase or decrease of $5^{\circ}\text{C}.$, excepting in the cases of the Upper Boreal and the Upper Austral.

This means that most species are, so far as known, confined to zones of amplitude of $5^{\circ}\text{C}.$ of summer temperature, that certain species extend over zones representing $10^{\circ}\text{C}.$ amplitude, while a few may extend over zones representing $15^{\circ}\text{C}.$ amplitude of summer temperature, and extremely few definitely known in zones covering over $20^{\circ}\text{C}.$ amplitude of summer temperature.

To mention the results of the preliminary survey of the marine *Rhodophyceae* so far listed and checked, may give approximate conditions which also seem to exist in other groups. The species and varieties thus far accredited to this group number about 3,350. Of these the northern hemisphere has about 34 per cent in its extratropical waters, the southern hemisphere approximately 44 per cent, while the tropical waters have approximately 22 per cent. Of the entire number, approximately 71 per cent are confined to one zone of temperature; about 21 per cent extend over two successive zones of different temperature; about 6 per cent are accredited to three successive zones of different temperature; while between 1 and 2 per cent are accredited, but with more or less, generally very considerable, doubt, to four, or even to five, successive zones of different temperature.

Commenting on the above, it may be surmised that the percentage in one zone is high on account of many new or little known species which have been collected only once, while the percentage of species occurring in two successive zones of different temperature is low because of our incomplete knowledge. Concerning the species credited to three zones, the percentage is small but perhaps not much lower than will be found on final careful revision. Here seasonal occurrence and "spot" distribution will undoubtedly be found to be concerned in the overlapping, as it will be also in the case of overlapping in two zones. Concerning the occurrence in four or five successive zones of different temperatures the percentage although small will, with very little doubt, be decidedly decreased or even entirely erased when the doubtful cases are investigated and cleared up. There may be a fraction of one per cent still left, however, and if there is, I doubt not that some fairly simple physiological explanation of their toleration of such an extreme range of temperature will be found. The disturbances in the uniformity of regular increase or decrease in the temperature of surface waters, as referred to latitude, have already been mentioned as due to cold upwellings and spot variation according to local physical peculiarities. These disturb, of course, the zonal distribution. Where such intrusive areas of colder or warmer water are extensive, the distribution in those areas must be considered in connection with the nearest zone of similar temperature. Spot distribution also, may be so referred but only in general considerations of distribution. Otherwise it must be considered specially.

The disturbance of regular zonal distribution which must have special consideration from the zonal point of view is that which arises from seasonal variation in the surface temperature accompanied by seasonal occurrence of a certain element of the flora in some district or province of a region of the particular zone.

Seasonable amplitude varying on an average from about 5°C. to 15°C. in extent, as I have mentioned before, is found in the various temperature zones. Seasonal duration, or, at

least increased seasonal vigor in certain elements of the flora is found in all zones, a phenomenon of mixed dependence upon light and temperature. It is most marked in the Temperate zones but is to be found in the Subtropical, Lower Boreal and Lower Austral zones as well. In the Upper Boreal and Upper Austral zones its appearance is perhaps more associated with varying intensity of light than with temperature, and it is least pronounced in the Tropical zone, where it seems to be wholly dependent upon light variation.

It is certain that many boreal summer species appear as winter or early spring species in the Temperate zone and likewise certain temperate species appear during the colder season in the Subtropical zone. There is some, but apparently not very much, overlapping between the upper portions of the Subtropical zones and the Tropical zone. From the very incomplete studies thus far made, it seems that most species range through from 5 to 10°C. of temperature, that each zone has its own characteristic species and that extensions up to 15°C. for active growth and reproduction are few, if at all existent. More careful examination, however, is necessary to satisfactorily demonstrate this last point.

While the limits of the temperature zones have been founded on the isotheres or lines of average daily summer temperature, seasonal phenomena cause us to consider also the isocrymes or lines of average daily winter temperature, especially as to overlapping or transitions between the zones. The isocrymes are of especial importance in those portions of certain zones where, especially on account of strong currents, the seasonal variation is extreme, e.g., on the eastern coast of North America and on the eastern coast of Asia. In such regions there may be expected extreme expression of seasonal change of flora.

The disturbances of distribution due to upwellings cause confusion in the tabulated results unless they are to be definitely accounted for. This confusion is greatest at present in connection with the species of the central coast of California. Spot distributions also cause the species concerned to be tabulated in more than one, or, if combined with seasonal disturb-

ance, over three zones. Spot distributions are less easy to detect than other anomalous distributions but enough are sufficiently known to make apparent their influence and importance in any scheme of representation of geographical distribution.

While the distribution of any particular species of plant depends upon a complex of conditions controlling continued existence, both vegetative and reproductive, certain more general factors may be distinguished as prevailing over larger areas, while others, less general, may account for local and usually discontinuous distribution within particular provinces and districts, and as components of various formations, bathymetric belts, and associations.

Temperature has come to be considered as one of the most important of the conditions controlling, or governing, the distribution of plants and animals (cf., e.g., Merriam, '94, '98, etc.; Livingston and Johnson, '13; and others). Any biologic factor has, of necessity, two variables (cf. Livingston and Johnson, '13, p. 351), intensity and duration, and these two variables present considerable range, especially in the case of land plants. For marine plants, particularly for those species constantly submerged, the amplitude of these variables is less than for the land plants. The surface waters of the ocean, while influenced by the temperature of the air, change slowly and only within certain limits. More considerable is the variation through the influence of varying, especially seasonal, currents or upwellings. Yet on the whole the temperature variables are seemingly, at least, much less in amplitude than are those of the land. For those plants exposed during tidal changes the temperature variables may be considerable in amplitude. Yet such exposures are only occasional and of short duration, except, perhaps, for the plants of the uppermost tide limits. One matter of importance as to all factors in plants submerged entirely or for the greater portion of the time, is the uniformity of exposure to the same conditions. While the land plant may have its roots buried in the soil of one temperature and its aerial organs exposed to a considerably different temperature, the entire

surface of the submerged plant is exposed to one and the same temperature. The problem, therefore, of temperature as a physiological factor in controlling the distribution of algae, in general, and of marine algae in particular, is, as compared with that of land plants or of land animals, comparatively simple.

Any attempt to unravel the physiological basis for the control of distribution must be, at this point of the progress of the work, lacking sufficient data for conviction. The statements presented merely represent approximate optimal conditions for the duration, succession, and, therefore, continued persistence of the species of the various life zones. It seems certain that the coefficients for continued existence vary among the different species, but are restricted in the case of each species to about $10^{\circ}\text{C}.$ in amplitude. There must be for each species a certain minimum and a maximum of optimal temperature for continued life and reproduction. It is possible that certain species may continue to exist outside these, especially if they possess powers of vegetative reproduction.

Thus far, it has been in mind to attempt to determine coefficients of efficiency as Livingston and Johnson have suggested in the case of climatic factors controlling the distribution of land plants, but no real beginning has, as yet, been made. The interval of $10^{\circ}\text{C}.$ certainly suggests the working of the van't Hoff-Arrhenius principle as applied to vital phenomena. Taking the variation of $10^{\circ}\text{C}.$ as the controlling interval of temperature and regarding it as an index to the summation of temperature, it may be possible in a later paper to definitely estimate the coefficients of temperature-efficiency in a fashion similar to that already suggested by Livingston and Johnson ('13) for land plants.

If the rate of the vital activities are, in general, doubled or nearly so with each increase of $10^{\circ}\text{C}.$, then, judging from the results of the *Rhodophyceae*, thus far tabulated, it would seem that marine algae cannot endure an acceleration greater than 2, that each species has its own definite initial temperature for efficient vegetative and reproductive activity and that such initial efficient activity may be accelerated up to the

doubling point, but not beyond it. In this way may be explained the fact that from 0°C. (or -2°C.) to 10°C. of mean summer temperature marks the limits of the Upper Boreal and Upper Austral zones. The marine algae inhabiting these zones are subjected to a range of not over 10°C. at any, or all, times. The species of the Temperate zones, enduring a mean summer temperature of 10°C. to 15°C. have a range of 10 to 12°C., probably not over, at any or all times. Similarly those of the Subtropical and Tropical zones endure a range of not over 10°C. If, therefore, tentatively, a temperature efficiency coefficient be estimated according to the formula of Livingston and Johnson ('13, p. 365) but modified by leaving out the assumption of an initial temperature higher than 0°C., viz., $u = 2 \frac{t}{10}$, the efficiency coefficient in the case of the Upper Boreal and the Upper Austral zones (0 to 10°C.) will be unity to 2, in case of the Lower Boreal and also the Lower Austral (10 to 15°C.), will be 2 to 3, for the Temperate zones (15 to 20°C.), the coefficients will be 3 to 4; for the Subtropical zones (20 to 25°C.), the coefficients will be 4 to 5, and for the Tropical zones (25 to 30°C.), the coefficients will be 5 to 6. Incidentally to carry out this idea of temperature efficiency coefficients, it may be said that the application to the case of thermal algae, where I find the 10°C. amplitude rule also to apply, would carry the coefficient index up as high as 16, i.e., in the case of those species enduring highest temperatures (80°C.), and even to 18 in the case of thermal bacteria (90°C.).

In conclusion, I may say that while much detail remains to be considered and brought into order before the final data and conclusions may be published, I have reason to believe that the statements and conclusions I have either made or brought forward in this preliminary account, will probably not need be changed, at least to any great extent.

LIST OF WORKS REFERRED TO

Börjesen, F. ('02). Marine algae. Botany of the Faeröes 339-532. f. 51-110. 1902.

———, ('05). The algae-vegetation of the Faeröese coasts with remarks on the phyto-geography. *Ibid.* 683-834. pl. 13-24. f. 151-164. 1905.

- , and Jónsson, H. ('05). The distribution of the marine algae of the Arctic Sea and of the northernmost part of the Atlantic. *Ibid.* Appendix: I-XXVIII. 1905.
- Collins, F. S. ('00). Preliminary lists of New England plants.—V. Marine algae. *Rhodora* 2:41-52. 1900.
- Cotton, A. D. ('12). Marine algae. Clare Island Survey, Part 15. *Roy. Irish Acad., Proc.* 31:1-178. *pl.* 1-11. 1912.
- Deutsche Seewarte-Hamburg ('92). *Indische Ozean, ein Atlas.*
- , ('96). *Stiller Ozean, ein Atlas.*
- , ('02). *Atlantischer Ozean, ein Atlas.* [2nd ed.]
- Farlow, W. G. ('81). Marine algae of New England and adjacent coast. U. S. Fish Comm. Rept. 1879:1-210. *pl.* 1-15. 1881.
- Gain, L. ('12). La flore algologique des régions antarctiques et subantarctiques. Deuxième Expédition Antarctique Française 1908-1910. *Sci. Nat. Doc. Sci.* 1-218. *pl.* 1-7. *f.* 1-98. 1912.
- Harvey, W. H. ('58). *Nereis Boreali-Americana.* Part I. *Melanospermeae.* Smithsonian Contr. 1-149. *pl.* 1-12. 1858.
- Hooker, J. D. ('45). The cryptogamic botany of the Antarctic voyage of H. M. Discovery Ships Erebus and Terror, etc. 1-258. *pl.* 57-198. 1845.
- Jónsson, H. ('01). The marine algae of Iceland (I. Rhodophyceae). *Bot. Tidskrift* 24:127-155. *f.* 1-4. 1901.
- , ('03). *Ibid.* (II. Phaeophyceae). *Ibid.* 25:141-195. *f.* 1-25. 1903.
- , ('03a). *Ibid.* (III. Chlorophyceae. IV. Cyanophyceae). *Ibid.* 337-385. *f.* 1-19. 1903.
- , ('04). The marine algae of East Greenland. *Meddelelser om Grönland* 30:1-73. *f.* 1-13. 1904.
- , ('12). The marine algal vegetation. In Warming, E., and Rosevinge, L. K., *The Botany of Iceland* 1:1-186. *f.* 1-7. 1912.
- Kjellman, F. R. ('83). The algae of the Arctic Sea. *Kongl. Sv. Vetensk.-Akad. Handl.* 20^e:1-351. *pl.* 1-31. 1883.
- , ('02). Om Algenvegetationen i Skelderviken och angränsande Kattegatts område. *Meddelanden från Kongl. Landbruksstyrelsen* 2:71-81. 1902.
- , ('06). Om främmande alger ilandrifna vid Sveriges västkust. *Arkiv f. Bot.* 5^{te}:1-10. 1906.
- Kylin, H. ('06). Biologiska jakttagelser rörande algfloran vid svenska västkusten. *Bot. Notiser* 1906:125-138. 1906.
- , ('07). Studien über die Algenflora der schwedischen Westküste. *Inaug. Diss.* 1-287. *pl.* 1-7. *f.* 1-43. 1907.
- Lemoine, Mme. Paul ('12). Sur les caracteres des genres *Melobesiees* arctiques et antarctiques. *Compt. rend. acad. Paris* 154:781-784. 1912.
- Livingston, B. E., and Johnson, Grace ('13). Temperature coefficients in plant geography and climatology. *Bot. Gaz.* 56:349-375. *f.* 1-3. 1913.
- Merriam, C. H. ('94). Laws of temperature control of the geographic distribution of terrestrial animals and plants. *Nat. Geog. Mag.* 6:229-338. 3 col. maps. 1894.

- , ('98). Life zones and crop zones of the United States. U. S. Dept. Agr., Biol. Survey, Bull. 10:1-33. 1898.
- Murray, G. ('93). A comparison of the marine floras of the warm Atlantic, Indian Ocean, and the Cape of Good Hope. Phycological Memoirs 2:65-69. 1893.
- , and Barton, E. S. ('95). A comparison of the Arctic and Antarctic marine floras. *Ibid.* 3:88-98. 1895.
- Oltmanns, F. ('05). Morphologie und Biologie der Algen 2:1-443. f. 468-617. 1905.
- Porsild, M. P., och Simmons, H. G. ('04). Om Faeröernes Havalgevegetationen og dens Oprindelse. En Kritik. Bot Notiser 1904:149-180. 1 map. 1904.
- Reinke, J. ('89). Algenflora der westlichen Ostsee, deutschen Antheils. Ber. d. Komm. z. wiss. Unters. d. deut. Meere in Kiel 6:III-XI and 1-101. f. 1-8. 1 col. map. 1889.
- Rosevinge, L. K. ('93). Grönlands Havalger. Meddelelser om Grönland 3:765-981. pl. 1-2. f. 1-57. 1893.
- , ('98). Om Algevegetationen ved Grönlands Kyster. *Ibid.* 20:131-242. f. 1-4. 1898.
- , ('98a). Deuxième mémoire sur les Algues du Groenland. *Ibid.* 1-125. pl. 1. f. 1-25. 1898.
- , ('98b). Sur la végétation d'algues marines sur les côtes du Grönland. *Ibid.* 339-346. 1898.
- Saunders, De A. ('01). Papers from the Harriman Alaska Expedition. XXV. The Algae. Wash. Acad. Sci., Proc. 3:391-486. pl. 43-62. 1901.
- Schmitz, Fr. ('96). Marine Florideen von Deutsch-Ostafrika. Bot. Jahrb. 21:137-177. 1896.
- Schroeder, B. ('12). Zellpflanzen Ostafrikas gesammelt auf der akademischen Studienfahrt, 1910. Hedwigia 52:288-315. 1912.
- Setchell, W. A. ('93). On the classification and geographical distribution of the Laminariaceae. Conn. Acad. Arts and Sci., Trans. 9:333-375. 1893.
- , and Gardner, N. L. ('03). Algae of northwestern America. Univ. Cal. Publ., Bot. 1:165-418. pl. 17-27. 1903.
- Simmons, H. G. ('97). Zur Kenntniss der Meeresalgen der Färöer. Hedwigia 36:247-276. 1897.
- , ('05). Remarks about the relations of the floras of the northern Atlantic, the Polar Sea, and the northern Pacific. Beih. bot. Centralb. 19²:149-194. 1906.
- Skottsberg, K. ('06). Observations on the vegetation of the Antarctic Sea. Bot. Studier 245-264. pl. 7-9. 1 map. 1906.
- , ('07). Zur Kenntniss der subantarktischen und antarktischen Meeresalgen. I. Phaeophyceae. Wiss. Ergebn. d. Schwedischen Südpolar-Exp. 1901-1903. 4:1-172. pl. 1-10. f. 1-187. 1907.
- Svedelius, N. ('01). Studier öfver Osterjöns Hafsalgflora. Inaug. Diss. 1-132. f. 1-26. Upsala, 1901.
- Yendo, K. ('02). The distribution of marine algae in Japan. Postelsia 1:177-192. pl. 19-21. 1902.

PHYTOPATHOLOGY IN THE TROPICS

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Tropical life is a luxurious life. Nowhere does plant and animal life show itself in such variety and abundance as on the equator.

As the conditions in those regions are uncommonly favorable to plant growth, it would appear that the plant parasites also have a good chance of living. In several tropical countries plant diseases have been studied in a more or less extensive way, but the general features of plant diseases in the tropics, unlike those of the temperate regions, have hardly been touched. I have been for some time studying plant diseases in our colonies of the East Indies, the so-called Malayan Archipelago, and I wish to give you some general impressions on fungous diseases in those countries. My remarks can be only suggestions, as thorough investigations on these tropical problems have never, so far as I know, been made.

The Malayan Isles have an average temperature of 30°C. in the lower parts, accompanied by a humidity of 80–100 per cent. The climate is a monsoon climate. In the time of the wet season it pours every afternoon, but in the dry time the rains are very scarce in the lowlands but not infrequent in the forest-covered mountains.

One would be inclined to think that this combination of high temperature and moisture would be extremely favorable for fungous growth, and that therefore fungous diseases would play a large part in the culture of economic plants. This, however, is not the case. We find that insect troubles prevail, and that, compared with our temperate regions, few diseases exist. We would not conclude these facts from the literature, as a large number of diseases caused by fungi have been described. But in visiting the countries it struck me that only a few diseases are of real importance; a great

many of those described must have been found occasionally, and have had no serious influence upon the cultivation of plants.

Not only among the cultivated plants do we find little fungous growth, but also in the natural vegetation. In the virgin woods the trees have few enemies among the fungi, and even the flora of mushrooms on the ground, so characteristic of our woods, is absent. Everything seems to point to the conclusion that conditions are unfavorable to fungous growth.

Why is this so? As has already been said, there are two conditions which characterize a tropical climate: (1) a high temperature which is about equal through all seasons, and (2) a high humidity, the latter varying somewhat in the different monsoons, but being altogether much higher than in our climates.

It seems to me that the tropical temperature is too high for many fungi. I cultivate in my laboratory over 600 fungi, and this collection shows clearly that the temperature of optimum growth of the greater part of the fungi lies beneath 30° C., often under 25° C. An exposure to high temperature prevents many parasites from forming their spores or fruiting bodies, whereas others require a change of temperature for normal growth. The *Polyporaceae*, for instance, bear exposure to frost very well, but many of them scarcely develop at 30° C. High temperature very often gives rise to an abnormally abundant mycelial growth, combined with an absence of spores. On the other hand, the high moisture content of the air must be favorable to fungous development.

But every fungous disease of plants involves two organisms, the parasite and the host, and the same conditions may influence these two in a very different way. The heavy rain-falls, combined with the abundant transpiration—owing to the intense heat, must cause a high water-content and a small air-content, of the wood-vessels of the trees, thereby making a substratum poor in air. We know that this is an important factor in fungous growth. This fact, combined with the high temperature, would explain the rare occurrences of *Hymenomycelae* and other wood-destroying fungi in the tropics.

I shall begin the consideration of the different groups of fungi which cause plant diseases in the tropics by mentioning one biological group of hymenomycetous fungi the members of which attack tropical cultivated plants. These are the so-called root fungi. It is certain that the root parasites belong to different species of *Hymenomycetae*, and that one species of host-plant may be attacked by a number of species of these fungi. Several of the latter, if not all, are characterized by the peculiar mycelium characteristic of the *Hymenomycetae*; in many cases, however, fruiting bodies have never been found. Practically all cultural woody plants—tea, coffee, rubber, quinine, cacao, coca—may suffer from the attacks of root-fungi, these attacks occurring mostly on virgin soil. The fungi develop on the decaying stumps of the forests, grow through the soil, and reach the roots and stem bases of the young tea, coffee, or quinine plant. The bark is penetrated and the mycelium destroys both bark and wood (the mycelium strands can be very clearly seen between bark and wood). Whereas young plants up to three or four years old nearly always are killed, older ones may resist; different species of plants, however, behave differently in this respect. In some districts the fruiting bodies of *Fomes semitostus* appear on the dying plant or on the dead roots, but in others fruiting bodies have never been found.

A second biological group of fungi, so common in our latitudes, has only a few representatives in the tropics under discussion. I am speaking of those ascogenous or imperfect fungi which cause the die-back diseases of our orchard, forest, and park trees, e.g., *Valsa*, *Diplodia*, and others. These fungi kill the branches by penetrating into the bark and sometimes into the wood. They appear on our trees when these are in a dry condition, and in dry climates or in dry years such diseases are of importance. Not so, however, in the tropics. The only die-back disease which is common is caused by *Corticium javanicum*, which, however, belongs to the *Hymenomycetae* and forms red layers on twigs, branches, and even trunks of all cultural woody plants, e. g., rubber, coffee, quinine, tea, cacao, coca, and fruit trees. We find the disease

mostly in very moist valleys, where the wind has no free play. The fruiting bodies of many *Ascomycetae* develop in dry air, and it is not remarkable that that type of disease is found in some parts of the West Indies, which have a drier climate.

A group which has no representative in the tropics is that of the powdery mildews (*Erysiphaceae*). These fungi occur only in colder climates. The so-called false mildews or *Peronosporaceae*, on the other hand, are of considerable importance, these fungi seeming to thrive well under the moist and hot weather conditions. We find the canker of rubber and cacao (caused by *Phytophthora Faberi*) of far-reaching importance. In both the rubber and the cacao the disease attacks the bark and, in the case of the cacao, also the fruit. The growth of this fungus depends upon a very moist air. This is proved by the fact that when the trees are cut back severely so that the trunk is exposed to sun and wind, the wounds often heal and the disease is stopped. A plantation in which the trees are planted far apart also suffers less.

Another fungus—*Phytophthora Nicotianae*—belonging to the *Peronosporaceae* is the cause of a dangerous tobacco disease. The parasite kills the seedlings in the beds, the plants “melt,” and even the mature tobacco plants are attacked. The fungus penetrates into the pith of the lower part of the stem and the “tobacco-tree” falls. A third member of this family destroys a large part of the Indian corn, so widely grown by the natives. It is *Peronospora Mayidis*, unknown, so far as I am aware, in the large corn areas of the United States. The exceedingly moist climate, combined with the excessive heat, evidently favors the attack by the fungus. In the potato fields of the mountain districts of Java we find a friend of our countries, *Phytophthora infestans*. Potatoes are grown in the tropics between 1500 and 6000 feet altitude. In the lower areas we find phytophthora-infected regions only rarely, but the higher we ascend, the lower the temperature (frosts may even occur in the nights) and the more destructive the phytophthora becomes. The spores of the fungus (it has been proved) cannot germinate at a high temperature, which explains the occurrence of the disease only in the higher

altitudes. It is very remarkable that in the tropics tubers are never, so far as I observed, affected. This fact might help us to discover the cause of the difference in susceptibility of the tubers of different potato varieties in our climate.

Speaking of potatoes, I wish to point out another disease of our regions which I found in the tropics and which has the greatest influence upon tropical potato culture. I am speaking of the internal brown spot, the nature of which has not been recognized. Nearly every potato tuber shows this disease and in a much more striking way than in the temperate regions. The brown spot is accompanied by a soft consistency of the tuber and a small amount of solid substance. As far as we know to-day, this trouble is a physiological one, caused by particular conditions of "climate and soil," the nature of which is unknown to us. The cause of the disease may be different in the tropics and in our regions, but a careful study of it in warm climates might give us an indication as to what conditions favor it.

Among the large group of rust-fungi, there is only one representative which is of importance to tropical agriculture. This is the coffee-leaf disease, due to *Hemileia vastatrix*, a rust which to a considerable degree ruined a large part of the coffee culture of Eastern Asia, and obliged the growers to introduce other species, which, unhappily, are of poorer quality. On other cultural plants, however, no rust of any importance occurs. The important cereal crop of the tropics, the rice, has no rust enemy. The rust of the sugar-cane is of no consequence in cane growing. The same is true of the smut diseases. Rice smut is found exceptionally, and smut of sugar-cane is a rarity; smut of corn is even rarer than in our regions.

Leaf spot diseases, belonging to ascogenous or imperfect fungi, are much less frequent than in Europe or the United States. The leaf spots of sugar-cane (*Leptosphaeria Sacchari*, *Cercospora Sacchari*, and *Cercospora Kophei*) are widely spread but have little influence on cane production. They are of more importance in the moist western part of Java than in the drier east. The tea blights (*Pestalozzia palmarum* and

Laestadia Theae) cause but small losses of tea leaves in our colonies.

The sugar-cane evidently is the crop which is most subject to the attack of fungi. This becomes clear when we look upon the method of propagating the saccharum. Small pieces of the cane stem are used as cuttings, which are put into the soil. The soft pith, rich in sugar, is an ideal substratum for fungous growth, and we must not be astonished that even saprophytes enter it. *Thielaviopsis ethacetica* and *Colletotrichum falcatum* are two typical destroyers of sugar-cane cuttings.

Bacterial diseases are scarcely to be found. I will admit that more bacterial diseases may be discovered, but up to the present time the only bacterial disease of importance is the tobacco wilt due to *Bacillus Solanacearum*, the same trouble which occurs in the United States. The same bacillus also causes a disease of peanuts. Probably the gum-disease of sugar-cane is also caused by bacteria. It is curious that algae in some cases (*Cephaleuros virescens*) cause diseases of tea and coffee plants, as they kill not only leaves but, as is true in the case of tea, also the twigs.

Here I have come to the end of the list of fungous troubles. Compared to the fungous diseases of the United States and even to those of Europe, those of the tropics are smaller in number. Tropical agriculture might be compared to the agriculture of the United States more than to that of the Old World. Vast areas are covered with one crop and often with one variety of a crop, so far as we know anything definite about varieties and races of tropical plants. In the subtropical regions of the United States, where at certain times the temperature equals that of the tropics, the air is much drier and there is a certain change of temperature, even in the region of eternal spring in California, which is foreign to the tropical climate. In the tropics of Asia and the subtropics of the United States insect troubles have assumed immense proportions, but as to fungous diseases, these are of more importance in the subtropics of the New World.

Different groups of fungi are much less restricted in their geographical distributions than are phanerogams. Up to the present time, no special tropical families among the fungi are known, and, as far as I know, the only fungus group that has no representatives in the tropics is that of the *Erysiphaceae*. The secondary part which fungi play in the plant diseases of the tropics is not caused by the absence of fungi, but by the particular conditions which influence both the host and the parasite, and their relations to each other. To establish the exact nature of these influences is a problem for the future.

PHYLOGENY AND RELATIONSHIPS IN THE ASCOMYCETES¹

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PART I. ARGUMENT

Perhaps there is no other large group of plants whose origin and phylogeny have given rise to such diametrically opposed hypotheses as the fungi. The presence of chlorophyll and the synthesis of carbohydrates from inorganic materials are such general and dominant characteristics of plants, that many students regard them as the fundamental traits which primarily marked the divergence of plant from animal life. According to this hypothesis all plants possess chlorophyll or were derived from chlorophyll-bearing ancestors.

No one questions the origin of the chlorophyllless seed plants from chlorophyll bearing ones by the loss of chlorophyll and reduction of photosynthetic organs.² What is more natural then, than the hypothesis that the fungi have been derived from chlorophyll-bearing ancestors? It is not my purpose to discuss the question as to whether or not the *Phycomycetes*, or lower fungi, had an independent origin, or were derived from one or several different groups of the green algae. I wish to consider some of the evidence which points to the origin of the *Ascomycetes* from fungus ancestry, rather than from the red algae.

¹ The first part of this paper is the abstract or argument as read at the anniversary proceedings. Because of the brief character of the abstract which renders many of the statements more or less categorical, while some therefore will appear dogmatic, the subject is further elaborated, and illumined by examples in a series of *Notes* which follow as an appendix in Part II.

² The chlorophyllless seed plants constitute comparatively small, isolated groups of separate origin from different families or orders of the spermatophytes. They do not constitute a phylum. The situation is quite different with the *Ascomycetes*, which make up a great phylum with ascending and diverging lines, as well as descending branches. They do not give evidence of many isolated groups derived by degeneration from many separate families of the red algae.

In this abstract the statements must be more or less categorical, and some will therefore appear rather dogmatic.

1. *The phylogenetic relation of the oöblastema filaments of the red algae, and the ascogenous threads of the sac fungi.*—The nuclear history in the two structures is very different. In the red algae there is a single fusion of one pair of sex nuclei in the egg, forming a true diploid nucleus which multiplies by division in the oöblastema filament providing the primary nucleus for each cystocarp. The oöblastema filament fuses with vegetative auxiliary cells to furnish attachment and base for food supply of the cystocarp, but the diploid and haploid nuclei of the fusion cell repel each other. The attempt to show a phyletic relation between the copulation of short oöblastema filaments with cells of the procarp, or the fusion of the procarp cells, after the union of haploid gametic nuclei, in some groups of red algae, and the communication of functional archicarp cells of certain sac fungi, as well as entertaining the notion that fusions of approximate cells of the ascogenous hyphae are phyletically related to the fusion of oöblastema filaments and auxiliary vegetative cells, introduces additional confusion into a doctrine already overburdened with questionable hypotheses. The oöblastema filaments and ascogenous threads are parallel developments. They present an example of morphological homology or analogy, not of phylogenetic affinity.

2. *The phylogenetic relation of the ascus and carpospore, or tetrasporangium* (see Part II, Notes II and III).—There are two horns to the dilemma here, and either one requires several additional supporting hypotheses. The origin of the ascus from a coenocytic zygote, in some cases by reduction, in others terminating a progressive splitting of the same, is far more comprehensible. The nuclear fusion in the ascus is not vegetative (see Note III). It takes place in all forms thus far investigated and is to be considered the final stage of the sexual act, however modified this may be. Were it merely vegetative fusion there would be no need of conjugate division in the ascus hook to avoid the union of sister nuclei. The nucleocytoplasmic relation, or balance, would be just as easily at-

tained by fusion of sister nuclei, or even by contemporaneous growth of nucleus and cytoplasm, such as is well known to occur in many other cases, for example in sexual cells, gonotokonts, etc.

3. *The phylogenetic relation of the ascocarp and cystocarp.*—If this principle of the resemblance between different types of cystocarp and ascocarp has any force, it would mean that the sac fungi had as many points of origin from the red algae as there are points of resemblance between their fruit structures. I presume no one at the present time holds any such view of the polyphyletic origin of the *Ascomycetes*.

4. *The phylogenetic relation of the trichogyne and sexual apparatus of the Ascomycetes and those of the red algae.*—The sexual apparatus of some of the *Ascomycetes*, particularly the trichogyne, and the so-called spermatia, is generally conceded to be the strongest evidence in support of their phyletic relation to the red algae. This theory, however, requires a jump from the simple trichogyne, a continuous prolongation of the egg of the red algae, to the complex, multi-septate one of the *Ascomycetes*. It requires further the reduction of this trichogyne to a unicellular one, and then to the simple gamete. It also requires the transition from free antheridia, or spermatia, to fixed ones, and from this specialized condition to the simple gamete, thus finally attaining the generalized condition of the copulation of simple gametangia. This appears to me to be a rather strained backward reading of the evidence.

ORIGIN OF THE ASCOMYCETES FROM FUNGUS ANCESTRY

Although Sachs' suggestion of the relation of the *Ascomycetes* to the red algae was received with favor by many students at that time, and the doctrine has received a fresh impetus in recent years, it was not accepted by some of the foremost students of the fungi at that time (Winter, '79; deBary, '84). DeBary plead for the application of the theory of descent which had come to be used as the basis of classification for the higher plants. As a result of his extensive studies of development in the *Phycomycetes* and *As-*

comycetes he was led to the conclusion that the *Ascomycetes* were derived from the *Phycomycetes*. This doctrine is based chiefly on the evidence of a phyletic relation between the sexual organs of the two groups. In spite of the persistence of the belief in the origin of the sac fungi from the red algae, deBary's doctrine of their descent from the *Phycomycetes* has had many adherents. Nowhere in deBary's writings have I been able to find any statement which can be construed as favoring the origin of the sac fungi from the red algae. The esteem in which his judgment is held, even at the present day, has led to the republication of a rumor of an *ante mortem* statement by deBary to the effect that he was inclined to the view that the procarps of the two groups pointed to the origin of the *Ascomycetes* from the *Rhodophyceae*!

Our present knowledge of the cytology of the ascus would not perhaps favor such close contact between the *Ascomycetes* and *Phycomycetes* as would appear from the knowledge possessed in deBary's time. Unfortunately we are not yet in possession of any cytological knowledge of spore production in the zygote of the *Phycomycetes* which we can use for comparison. But at any rate, the difficulties in this relation are no greater than are met with in attempting to derive the ascus from the carpospore or tetrasporangium of the red algae.

Origin of the ascogenous threads.—The ascogenous threads are outgrowths of the zygote or oögonium and represent one method of splitting up and proliferation of the same in accordance with recognized principles of progression in the same direction of increase in the output of spores following the sexual process, or its equivalent, and terminating the diploid phase.

One of the most instructive forms suggesting a mode of transition from the *Phycomycetes* to the *Ascomycetes*, is *Dipodascus*. Its sexual organs are strikingly like those of certain *Mucorales* or *Peronosporales* in their young stages. The sexual organs, which can be recognized as antheridium and oögonium, arise either from adjacent cells of the same thread, or from different threads. After resorption of the wall at the point of contact, the fertilized oögonium (or zygote) grows

out into an elongate stout "ascus" or zyogogametangium with the production of numerous spores. While all phases of the nuclear phenomena have not yet been made clear, the gametes are multinucleate, and multiplication either of the sex nuclei, or of the fusion nucleus, takes place in the generalized "ascus." This so-called ascus is an outgrowth of the undifferentiated oögonium or ascogonium. The splitting up of such a generalized ascus by filamentous outgrowths, the ascogenous threads, which branch and produce terminal asci containing fewer spores, would be a very natural course in progressive evolution, specialization, and increase in spore output.

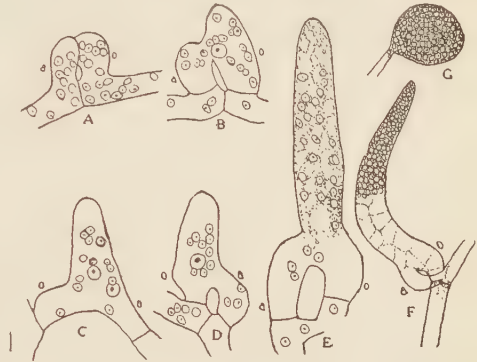


Fig. 1. *Dipodascus albidus*: A, copulation of gametangia; B, communication established between antheridium and oögonium; C, the two sex nuclei approaching each other; D, fusion nucleus large, vegetative nuclei small; E, growth of generalized ascus from oögonium side of copulating gametes, early stages of, in C and D; F, generalized ascus with numerous spores; G, spore mass crowded out of end of ascus. a, antheridium; o, oögonium.—A-E, after Juel; F and G, after Lagerheim.

Origin of the ascus in the Endomycetaceae.—The tendency of generalized forms to split up in different directions, often giving rise to divergent lines or series, is a well founded principle in the doctrine of descent. These series are often of different character in respect to numbers and diversity of forms, as well as to progression or reduction in one or more structures. One of the directions in which descent from such a generalized, coenocytic, germinating zygote (or ascus) as represented by *Dipodascus* has taken place is that of reduction in size of the generalized ascus and in the number of spores. Evidence of this reduction is furnished by *Dipodascus* itself; for, as the culture ages the asci become smaller and smaller and the spores fewer in number. In this way by reduction in number of spores to 8 and 4, just permitting the meiotic nuclear divisions, forms like *Eremascus* and *Endomyces* have

arisen. Further reduction of one of the gametes, or of the vegetative stages, would result in apogamous forms of *Endomyces*, the *Exoasceae*,¹ the *Saccharomycetes*, or yeasts, etc. By reduction and loss of one of the gametes without reduction in size of the generalized "ascus," such forms as *Ascoidea*, *Protomyces*, *Taphridium*, etc., may have arisen.

Origin, progression and sterilization of the so-called trichogyne.—There is no well developed trichogyne-like structure in any of the known *Phycomycetes*. But there is evidence in a

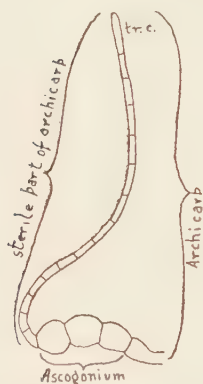


Fig. 2. Diagrammatic representation of the archicarp of lichens and many other *Ascomycetes*. The fertile part is the ascogonium; the sterile portion is the so-called "trichogyne"; tr.c, trichogyne cell.

few of the forms, like certain species of *Cystopus*, of a tendency of the oögonium, probably under chemotactic stimulation and a softening of the wall, to develop a short process directed toward the antheridium. This has been suggested by a number of students (Lotsy, '07, p. 468) to be an indication of the origin of the trichogyne in the *Ascomycetes*. It does not mean that *Cystopus*² is to be regarded as an ancestral form of the *Ascomycetes*, though certain species do possess a number of peculiarities which may be attributed to such a hypothetical form. This peculiar feature of the oögonium of some species of *Cystopus* is, however, of importance as it indicates one probable method of origin of the trichogyne in the *Ascomycetes*. The trichogyne is not a character possessed by all *Ascomycetes*, even of those which still retain two functional gametangia.

This, I believe, is strong evidence of the independent origin of the trichogyne in the *Ascomycetes*.

It arose as a copulating process or beak from the oögonium

¹ Such an origin for the *Exoasceae* is more comprehensible than the theory that their mycelium may represent ascogenous hyphae which have migrated from the condition of parasitism in the vegetative portion of a former ascocarp, to parasitism on their present hosts, as suggested by Harper ('00, p. 392).

² One of these features is the generalized character of the sexual organs, which are polyenergid, but particularly the great variation in number of functional egg nuclei in different species as described by Stevens ('99, '01).

under chemotactic stimulation, combined with a transverse splitting of the oögonium or archicarp.

The failure of the antheridium to perform its function in the sexual process, its reduction or loss, are well known features in the life history of a number of *Ascomycetes*. In many cases where the antheridium or its supposed equivalent, the spermatium, is to all appearance potentially functional, its failure to function appears to be due to the sterilization of the terminal portion of the archicarp.¹

Analogous situations are known in the seed plants. I need only cite the case of *Elatostoma acuminatum* (see Strasburger, '09). The nucleus of the embryo sac mother cell enters the preliminary phases of the heterotypic division. After synapsis the further stages of the heterotypic division are inhibited, and by typic or "vegetative" division the eight-nucleated embryo sac is formed. The egg, therefore, ripens with a diploid nucleus, and, without fertilization, develops the embryo. The walls of the inner integument grow together at the micropylar end of the ovule and harden, thus forming an effectual barrier to the entrance of the pollen tube (Treub, '05; Strasburger, '09). While great disturbances occur in pollen development and most of the pollen grains are empty or undeveloped, some pollen is formed which appears normal. In some cases the mother cell, which usually forms the diploid embryo sac, undergoes a true reduction division forming a row of four cells, the lower one of which forms a normal embryo sac with a haploid egg. The few male plants of this species, Strasburger thinks, result from fertilization of such

¹ While the "trichogyne" or terminal portion of the archicarp assumed vegetative characters in an increasing degree, it seems that it did not in every case lose all of the features appropriate to a receptive organ. It appears in a few cases at least to still respond to chemotactic or analogous stimuli, seeking the fixed spermatia as in *Collema pulposum* (according to Bachmann, '13) and *Zodionomyces vorticellarius* (Thaxter, '96). In a number of cases there seem to be receptive areas on the trichogyne where the free sperms become fixed, where fusion of sperm and trichogyne takes place. The perforation of the transverse walls of the trichogyne, which is said to occur after fusion with the sperm, also appears to be another example of the retention of an ancestral character of the archicarp which primarily permitted the passage of sperm nuclei through the terminal segment, or the association of nuclei of different segments as parthenogenesis or apogamy was introduced.

haploid eggs by sperms from the normal pollen.

This sterility of the archicarp, I believe, has been brought about by its assumption more and more of a vegetative character. The formation of septa at the base of the "trichogyne" in such forms as *Pyronema* and *Monascus*, which primarily may have been the beginning of a transverse splitting of the oogonium, would make more difficult the fertilization of the basal portion of the archicarp. In *Aspergillus repens* the so-called "trichogyne," or terminal cell of the archicarp, sometimes gives rise to ascogenous hyphae¹ (according to Miss Dale, '09). The basal portion of the two-celled archicarp, or the basal or central portions of the several-celled archicarp, seem to be the portions which have retained the function of ascogenic cells where that function still resides in the archicarp. As the archicarp becomes longer, the sterile portion, which is non-ascogenic, becomes longer and more septate. This only increases the difficulties of the passage of the sperm nuclei.

The increasing vegetative character of the terminal portion of the archicarp has given rise to the long, simple, multiseptate "trichogyne" of the lichens and many *Pyrenomyces* and *Discomycetes*, as well as to the profusely branched multiseptate trichogyne of certain *Laboulbeniales*.² It is an interesting fact that in many of the cases of the extraordinary vegetative development of the terminal portion of the archicarp (the "trichogyne"), antheridia and spermatia are entirely wanting.³

The degeneration changes of the sterile portion of the archicarp (multiseptate and often also much branched "trichogyne") which are described as taking place after connection of the spermatium with the receptive terminal cell (for lichens see

¹ It is worthy of note in this connection that Olive's studies ('05) of *Monascus* led him to regard the "trichogyne," or terminal cell of the archicarp, as the ascogonium, and the second cell, or ascogonium according to others, as a nurse cell.

² Thaxter ('96) says that when the spermatia do not become attached to the receptive cell of the trichogyne the vegetative growth of the trichogyne is greatly increased.

³ (*Lachnea cretea*, according to Fraser, '13; in *Teratomyces actobii*, Thaxter, '96, was not able to find antheridia.)

Stahl, '77, Baur, '98, Bachmann, '13; for the *Laboulbeniales*, Thaxter, '96, p. 225), may be classed as secondary or accompanying sexual phenomena. It does not necessarily follow that the sperm nucleus reaches the egg or fertile portion of the archicarp. The trichogyne changes taking place after the entrance of the sperm into, or its connection with the receptive terminal cell, are not dependent on the final fate of the sperm, i. e., whether it reaches the egg or not. They are antecedent phenomena and in no sense a proof that fertilization has taken place. These disintegration changes, initiated, it would seem, by the influence of the sperm on the receptive cell of the archicarp, terminate the vegetative growth of the archicarp and thus the reflex upon the fertile portion at the middle or base releases the ascogenic cells from the inhibiting influence of the vegetative phenomena, and they then proceed with the modified sexual process among the ascogonial nuclei which may be now associated in sexual pairs, or this pairing be postponed to some period in the development of the ascogenous hyphae.

Origin of spermatia in the Ascomycetes.—The presence of the so-called spermatia in many lichens and other *Ascomycetes*, associated at the same time in numerous instances with the trichogyne-like termination of the archicarp, is one of the major pieces of evidence brought forward in supporting the doctrine of the red algal origin of the sac fungi. If we accept this doctrine, then in the *Ascomycetes* we must read the history of the antheridia in the following order: They appeared first as free structures, spermatia, abjoined from spermatophores, large numbers of which were crowded in highly specialized receptacles.

At the next step there were few, imbedded, isolated antheridiophores to which a few spermatia remained attached, until finally the stage was reached where spermatium and antheridiophore were merged into the simple antheridium. This doctrine also requires that along with the change from free spermatia to the simple antheridium, there was a transition from the condition in which the spermatia do not function to

that where the sperm nuclei of the simple antheridium are functional.

Notwithstanding this interesting course of evolution of the antheridium and of sexuality which we trace if the red algae are accepted as the source of the *Ascomycetes*, I believe, just as in the case of the archicarp and trichogyne, the evidence warrants us rather in reading it in just the opposite direction; and that in the last stages of progressive development of the sexual apparatus in the *Ascomycetes*, the resemblances to the sexual apparatus of the red algae are merely those of morphological homology and analogy, not phylogenetic homology and affinity.

According to this view, then, the ancestral forms of the *Ascomycetes* were fungi with well developed, simple but generalized gametangia. This condition is retained in a number of existing *Ascomycetes*, in many of which true sexuality exists.¹

In connection with the specialization of the antheridium and the origin of the spermatia of the *Ascomycetes*, *Monascus* is an extremely interesting form. The antheridium is an elongate terminal cell of a hypha. The archicarp arises as a branch below the septum. It curves closely against the antheridium, bending it over more or less at right angles, and copulates at any point along the side of the antheridium, there being no portion of the latter especially selected as a copulation place. The conidia in *Monascus* are formed in chains by constriction and septation of terminal portions of hyphae similar in diameter to the antheridium. The archicarp sometimes copulates with a conidium of the chain before their final separation (Barker, '03). A chain of conidia is thus homologous with the antheridium, and a conidium with any section of the antheridium. It would be but a step from this condi-

¹ Examples of generalized, simple (non-septate) gametangia are found in *Dipodascus* and *Gymnoascus*. Examples of simple specialized gametangia, i. e., uninucleate gametangia, are found in the powdery mildews (*Erysiphaceae*) and *Eremascus*. A second stage is presented in forms where the antheridium remains simple and generalized, but there is a beginning of specialization in the archicarp where it is split transversely into two cells, the terminal one (trichogyne) functioning as a copulating organ and migration tube for the sperm nuclei. Examples are found in *Pyronema* and *Monascus*.

tion to the copulation of the archicarp with free conidia. The situation in *Collema pulposum* (Bachmann, '13), *Ascobolus carbonarius* (Dodge, '14), and *Zodiomyces vorticellarius* (Thaxter, '96), is similar where the trichogyne copulates with spermatia (conidia) still attached to the spermatophore. These cases are very strong evidence suggesting the homology of conidia (or pycnospores as the case may be) and spermatia¹ in the *Ascomycetes*.

Progression in the direction of multiplication of antheridia, or spermatophores, and their association in groups followed from the simple and more or less isolated situation, progressing along the same course which is recognized in the association

and massing of conidiophores into bundles, cushions, or pycnidia. It is the same course which is universally recognized as a striking indication of progression in other groups of plants, a *cephalization* of fruiting or reproductive structures, as in the bryophytes, lycopods, conifers, and angiosperms. In the latter it has given us the flower, and further cephalization of the flower has resulted in the head of the com-

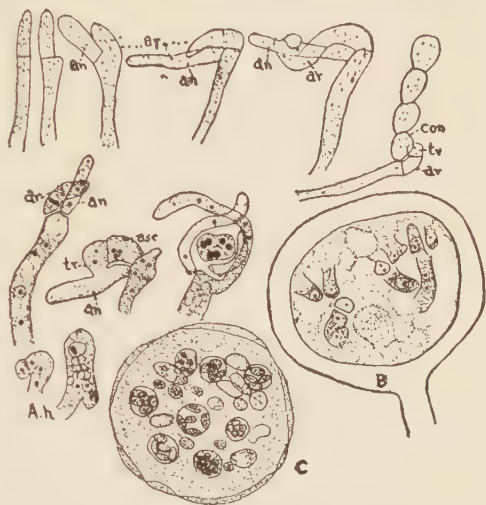


Fig. 3. *Monascus*, showing development of sexual organs and fruit. *an*, antheridium; *ar*, archicarp; *tr*, trichogyne; *asc*, ascogonium; *con*, conidium with which trichogyne is copulating; *A.h*, ascus hooks or croziers; *B*, young fruit showing ascogenous hyphae within, at left is a very young fruit body showing ascogonium becoming surrounded by the enveloping filaments; *C*, mature fruit body with asci and ascospores.—Upper row of figures after Barker; lower group after Schikorra.

¹ Their function in the ancestral or early forms may have been generalized enough to permit of their performing as conidia or sperms, as in the case of *Ectocarpus*, *Prostosiphon*, *Ulothrix*, etc. Strasburger ('05, p. 25) has expressed the idea that the pycnospores of the *Ascomycetes* might have been spermatia, and that the process of fructification now presented by these fungi is a secondary adaptation in place of the erstwhile fertilization by spermatia.

posites, the highest stage of phyletic evolution in the plant world.

In conclusion, the *Ascomycetes* present a very rich variety of form, structure, and adaptation with very marked diverging series. Some of these series present evidences of progression from simple, generalized forms to highly specialized forms, while others indicate descent by reduction. The evidences of progression are of the same kind and value as are generally recognized in other groups of plants.

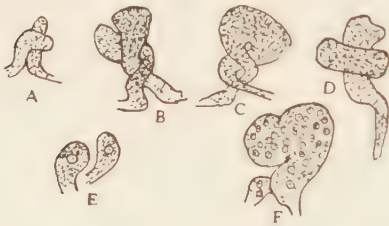


Fig. 4. *Gymnoascus Reessii*: A-D, formation of sexual organs, fusing at C; E, sexual organs in uninucleate condition; F, fusing sexual organs in multinucleate stage.—After Dale.

Sachs, in his later writings, agreed with deBary in recognizing the *Ascomycetes* as a distinct phylum, with an ascending series from simple and generalized forms to complex and specialized ones. He never mentioned the trichogyne as evidence of their phyletic relation to the red algae.

But his theory was based on the presence of a *procarp* whether with or without a trichogyne. He selected *Gymnoascus*, where the sexual apparatus consists of simple copulating gametangia, as the simplest ascomycete known at that time. It is only in recent years that the trichogyne has been seized upon as evidence of the phyletic relation of the two groups and has forced this anomalous backward reading of the history.

PART II. ELUCIDATION

NOTE I

The red algae are remarkable for the great constancy in the form of the *procarp* (*procarpic branch*, *carpogonial branch*, etc.) and the very great divergence in the processes subsequent to the fertilization of the egg (terminal cell of the *procarp*, *carpogonium*) and ending in the production of the *carpospores*. The general character of this divergence may be shown by a brief presentation of several types, as follows:

1. The simplest type of cystocarp development occurs in the *Nemalionales* where the carpogonium, or egg cell, after fertilization, gives rise to several branched sporogenous threads in a compact cluster, bearing terminally the carpospores (*Nemalion*, *Lemanea*, etc.), or in some species the sporogenous threads are more widely extended in the thallus, the branches producing separated clusters of carpospores (*Dermonea dichotomum*, see Schmitz and Hauptfleisch, '97). Fertilization by the fusion of a sperm nucleus with the egg nucleus after entrance into the trichogyne and migration down into the carpogonium has been described in *Nemalion* (Wolfe, '04) and in *Batrachospermum* (Schmidle, '99; Osterhout, '00).

2. In *Polysiphonia* (*Rhodomeniales*) the procarp branch of four cells is curved around so that the carpogonium is in contact with an auxiliary cell lying between the carpogonium and the pericentral cell which gave rise to the procarp. After fusion of the sperm and egg nucleus in the carpogonium, the fusion nucleus divides once. The carpogonium now connects with the auxiliary cell mentioned, which fuses with the pericentral cell. The two diploid nuclei migrate into the pericentral cell, the carpogonium separates from the auxiliary cell, while it and the remaining cells of the procarp degenerate. The pericentral cell now fuses with several other auxiliary cells, which arose from it as a branch, forming the central cell. The diploid nuclei remain in the upper part of the central cell, while the haploid nuclei from the auxiliary cells, some having divided, now degenerate (Yamanouchi, '06).

3. A somewhat different situation exists in *Erythrophyllum delesseroide* (*Gigartinales*). The oöblastema filament from the fertilized egg connects with the auxiliary cell which is the basal cell of the seven or eight-celled pro-

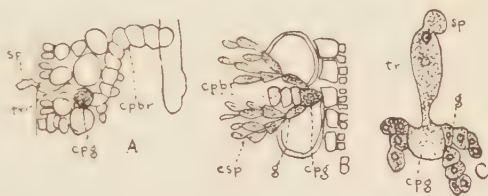


Fig. 5. A and B, *Lemanea*; C, *Batrachospermum*: cpbr, procarp or carpogonial branch; cp, carpogonium or egg; tr, trichogyne; sp, spermatium; g, gonimoblast; csp, carpospores. —A and B, after Atkinson; C, after Davis.

carp. This in turn fuses with the two other large cells of the basal portion of the procarp, thus forming the large fusion cell from which the

gonimoblasts, or sporogenous threads arise (Twiss, '11).

4. In *Harveyella mirabilis*,¹ a large cell which gives rise to the four-celled procarp is the auxiliary cell. A short oöblastema filament from the egg connects with the latter, which becomes the central cell.

5. In *Callithamnion* (*Ceramiales*) the fusion (diploid) nucleus in the egg divides into two. Two short oöblastema filaments proceed from

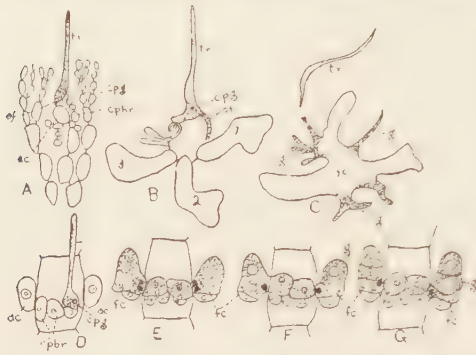


Fig. 6. A, *Harveyella mirabilis*; B and C, *Erythrophyllum delesseroidei*; D, E, F, and G, *Callithamnion corymbosum*: cpbr, carpegonium branch; cpg, carpegonium; tr, trichogyne; of, oöblastema filament; ac, auxiliary cell; g, gonimoblast; fc, fusion cell. 1, 2, and 3 are the three large basal cells of the procarp in *Erythrophyllum* which fuse with the oöblastema filament to form the fusion cell. Shaded portions are diploid; note that in the fusion cell of *Callithamnion* the vegetative nucleus (haploid) remains at a distance from the diploid nucleus.—A, after Sturch; B and C, after Twiss; D, E, F, and G, after Oltmanns.

the carpegonium, each containing a diploid nucleus, and fusing with an auxiliary cell at the side of the base of the procarp. Each of the two auxiliary cells now contains two nuclei. A wall divides each cell into two. The upper daughter cell contains the diploid nucleus and becomes the central cell, giving rise to the sporogenous threads, while the haploid nucleus in the lower cell degenerates (Oltmanns, '04).

6. The most complicated type may be represented by *Dudresnaya purpurifera* (*Cryptonemiales*) where several oöblastema filaments arise from the sterilized egg cell. These fuse with auxiliary cells which are either certain cells of the procarp branch, or terminal cells of its branched system, or of more distant "secondary procarp branches." An oöbla-

¹ *H. mirabilis* is parasitic on certain species of *Polysiphonia*, and is devoid of chlorophyll. For this reason it is regarded by some as indicating a step in the direction of an ascomycete.

stema filament after fusing with one auxiliary cell may grow forward and fuse with another and so on. The diploid nucleus formed in the egg multiplies by division in the oöblastema filaments. In the fusion cell, resulting from the union of the filament and auxiliary cell, the diploid and haploid nuclei repel each other so that the former lies on the filament side while the latter lies in the base of the auxiliary cell. An outgrowth

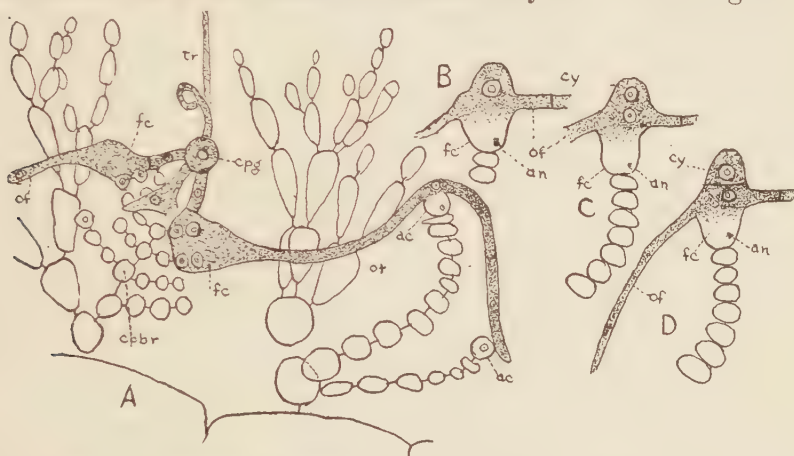


Fig. 7. *Duderneya purpurifera*: A, oöblastema filaments fusing with auxiliary cells; B, C and D, outgrowth from the fusion cell to form the central cell; C, diploid nucleus dividing; D, central cell of cystocarp separated by a wall. Note that the nucleus of the auxiliary cell remains distant from the diploid nucleus of the oöblastema filament. Shaded portions are diploid. cpbr, carpogenic branch; cpg, carpogonium; tr, trichogyne; of, oöblastema filament; fc, fusion cell; ac, auxiliary cell; an, auxiliary cell nucleus; cy, central cell of cystocarp.—After Oltmanns.

arises from the oöblastema filament at the point where the diploid nucleus lies. The latter divides, one nucleus migrating into the outgrowth, while a wall separates it from the fusion cell. This new cell with its diploid nucleus becomes the central cell (Oltmanns, '04).

7. In *Cruoriopsis cruciata* the situation is similar. The oöblastema filament by coursing widely through the thallus, fuses with the terminal cell (auxiliary cell) of "secondary procarp branches." Each of these fusion cells, or auxiliary cells, then gives rise to one or two simple rows of 2-4 spores (Schmitz, '79, '83), or a single 2-4-celled spore chain (Oltmanns, '04).

Relation between the fusions of procarp and auxiliary cells, and those of archicarp cells.—Several persons have made the interesting suggestion that certain similarities between the events which take place in the fusion of one or more of the middle or basal cells of the procarp with an outgrowth from the carpogonium, either direct, or through the medium of an auxiliary cell, as represented in *Erythrophyllum*, *Harveyella*, *Callithamnion*, etc. (third, fourth and fifth types mentioned above), and those occurring in the fusion among themselves of the middle or basal cells of the archicarp prior to the formation of the ascogenous threads, may be evidence of a phylogenetic relationship between the red algae and *Ascomycetes*. Thus Baur ('98) suggests that the first fertile cell of the several-celled ascogone of *Collema crispum* may be the egg cell, that this may be fertilized by the entrance of the sperm nucleus and its fusion with the egg nucleus. This fusion nucleus may now divide. The other cells of the ascogone below the egg are conceived of as auxiliary cells into each one of which a nucleus resulting from the division of the fertilized egg nucleus migrates after pore formation in the intervening walls.

In an interesting paper on the morphological relationships of the *Florideae* and *Ascomycetes*, Dodge ('14) emphasizes this theory by pointing to a number of cases in the lichens and other *Ascomycetes* where fusion, or pore connections, are known to occur between the ascogenous cells of the archicarp where more than one cell gives rise to ascogenous hyphae. Examples among the lichens are *Collema crispum* (Baur, '98), *Phycia pulverulenta* (Darbishire, '00), *Anaptychia ciliaris* (Baur, '04), and *Collema pulposum* (Bachmann, '13), while among the other *Ascomycetes* may be mentioned the following: *Ascobolus* (Harper, '96. Here there is but one ascogenous cell which gives rise to the ascogenous hyphae, but pore formation in intervening walls permits intercommunication between several adjacent cells in the middle of the archicarp. The species is not given), *Ascophanus carneus* (Cutting, '09), *Lachnea cretea* (Fraser, '13), *Polystigma rubrum* (Nienburg, '14).

Now as to the suggested relationship between the phenomenon of broad or narrow pore formation in the walls of certain cells near the middle or base of the archicarp in certain lichens and other *Ascomycetes*, and that shown in the communications taking place between the carpogonium and auxiliary cells (often including one or more of the other procarp cells), it may be said (1) that in the red algae this communication of the carpogonium (terminal procarp cell) with other procarp cells when it does take place is not direct, but by a roundabout method, either through a distinct outgrowth from the carpogonium, or through the medium of one or more auxiliary cells, or by a combination of both, to form the central cell; (2) no evidence of any similar roundabout method has been observed in the archicarp of the sac fungi. The intercommunication between the middle or basal cells of the archicarp is always direct, and no communication in the multicellular archicarp occurs by means of which either a fertilized nucleus, or a sperm nucleus has been observed to migrate from the terminal cell to the middle or basal cells; (3) that in a number of the fungi where pore formation occurs between cells of the fertile portion of the archicarp, the "trichogyne" is either absent, or admittedly degenerate, or the antheridium is absent. Examples are: *Ascobolus*, studied by Harper ('96), antheridium and trichogyne absent; *Ascophanus carneus*, antheridium absent, trichogyne doubtful or degenerate; *Lachnea cretea*, no antheridium observed, trichogyne not functional; *Polystigma rubrum*,¹ trichogyne not functional, from a multicellular cell at base of archicarp one nucleus migrates into the adjacent uninucleate archicarp cell, which is regarded as the ascogonium (Nienburg, '14). In none of the lichens has a sperm or other nucleus been observed to move down into the fertile part of the archicarp. Pore formation in the archicarp of the *Ascomycetes* has no phyletic relation to the fusions of auxiliary cells among themselves or with a short oöblastema thread or the egg cell. It occurs in-

¹ Blackman and Welsford ('12), who earlier investigated the cytology of *Polystigma rubrum*, are of the opinion that the "spermatia" as well as the archicarps degenerate, and that certain vegetative cells become transformed into ascogones.

dependently in different groups of the fungi as a means of permitting the association of nuclei, often in conjunction with the association of sex nuclei or their equivalent modified sex nuclei (see the situation in *Basidiobolus*, Eidam, '86; Raciborski, '96; Fairchild, '97; Olive, '07; Woyciecki, '04).

Relation of oöblastema filaments and ascogenous hyphae.—In the *Ascomycetes* the processes in the growth of the zygote or ascogenic cell present to a certain extent a somewhat analogous course of progression to that of the carpogenic cell of the red algae. In the less complicated process, as shown in the *Laboulbeniales*, the carpogenic cell may undergo a few divisions, the subterminal cell of the series forming the ascogonium. The ascogonium then usually divides to form two or four ascogenic cells, or without division forms the single ascogenic cell (Thaxter, '96; Faull, '12). The ascogenic cells give rise directly, by budding, to the asci. They are, therefore, somewhat comparable or analogous to the gonimoblasts of the red algae. In *Sphaerotheca* (Harper, '95^a, p. 475) there is a single short ascogenous thread of a few cells (arising from the one-celled oögonium or ascogonium) forming a single ascus from the subterminal cell. Where the process is more complex, as in *Pyronema* (Harper, '00; Claussen, '12), several long ascogenous hyphae arise from the large single-celled zygote or ascogonium, giving rise ultimately to numerous terminal asci. In other forms the ascogonium is several-celled, a number of the cells developing ascogenous hyphae (*Collema*, Stahl, '77; Baur, '98; Bachmann, '12, '13; *Anaptychia ciliaris*, Baur, '04; *Physcia pulverulenta*, Darbishire, '00; *Ascophanus carneus*, Cutting, '09; *Lachnea cretea*, Fraser, '13; etc.).

Some of the chief objections in the way of accepting the theory of a phylogenetic relation between the oöblastema filaments of the red algae and the ascogenous threads of the sac fungi are as follows:

1. The fusion of a free sperm and the egg nucleus in the single uninucleate oögonium or carpogenic cell. So far as we know this is universal in the red algae. In the *Ascomycetes* the oögonium is usually multinucleate or multiseptate. In no

case has fertilization by a free sperm been determined, and in forms with a multiseptate "trichogyne," or oögonium, the so-called spermatia, or antheridia, do not, so far as we know, play the usual rôle in fertilization, not even a modified rôle by association with the oögonial nuclei.

2. The individual nuclei of the oöblastema filaments are of the usual diploid character, and there is no fusion of these nuclei prior to the formation of the carpospores. The individual nuclei of the ascogenous threads, or ascogenic cells, are probably haploid in character, and sooner or later form the so-called synkarion, an association of two nuclei, together equivalent to a diploid nucleus. Fusion of the paired nuclei takes place before the formation of the ascospores.

3. It has been suggested that the complex processes in the extensive migration, branching and fusions of the oöblastema filaments with auxiliary cells as is known to occur in the *Cryptonemiales* (as in *Dudresnaya*, *Cruoriopsis*, *Gloeosiphonia*, etc.), may furnish still more important evidence of the ancestry of the *Ascomycetes* than that suggested in the fusions of procarp and auxiliary cells on the one hand, and archicarp cells on the other (Dodge, '14). The fusions of the oöblastema filaments with auxiliary cells and the production of sporogenous threads from the central cells thus formed, are supposed to be represented by the fusions which are known to occur between the ultimate and antepenult cells of the ascus hook prior to the formation of additional asci. The processes in both groups result in the multiplication of spore origins and consequently in an increase in spore output. Perhaps the nearest analogue to the process in the *Ascomycetes* which results in the formation of the ascus with its four to eight spores, is found in *Cruoriopsis*, where one or two spore chains of two to four spores each are produced as a result (Schmitz, '79, '83; Oltmanns, '04). The theory of "second sexual fusions" in the red algae was founded on the discovery of these fusions of the oöblastema filaments with auxiliary cells, since it was supposed that a fusion occurred between the nucleus of the oöblastema filament (derived from the diploid nucleus of the fertilized egg) and the nucleus of the vegetative auxiliary cell

(Schmitz, '83). Recent cytological work on the red algae has not confirmed this theory, but, on the other hand, has discredited it, since in the cases examined the diploid nucleus of the oöblastema filament and the haploid nucleus of the auxiliary cell are said to repel each other and no fusion between them occurs. It should be emphasized that the fusion of the oöblastema filament and the auxiliary cell is a fusion of a diploid structure with a haploid one, that it is probably of a nutritive, or parasitic, nature comparable to the fusion of the moss sporogonium with the tissue of the gametophyte, a physiological, nutritive requirement in the absence of other means of nourishing the moss sporogonium. The fusions occurring between cells of the same ascogenous hypha are fusions between cells of the same phase and serve to bring into association nuclei of more or less remote ancestry, but each endowed with the same number of chromosomes (probably the $1x$ number).

Thus, while there are somewhat analogous variations in the splitting up of the ascogonium in the sac fungi, and of the carpogonium in the red algae, with progress in the direction of increasing the output of spores, it seems fair to conclude, that, so far as the evidence at present in hand is concerned, the relation between the fusion of oöblastema filaments and auxiliary cells in the red algae, and those between the ultimate and antepenult cells of the ascus hook (of the ascogenous hyphae), however interesting it may be, has no phylogenetic significance, and is at best a rather strained parallel.

Ascogenous hyphae, gonimoblasts, oöblastema filaments, the several fertile cells of certain ascogonia which communicate by resorption of the intervening septa, the fused procarp, may be considered as morphological equivalents, as suggested by Dodge ('14, p. 174), but there is no evidence of a phyletic relation between the ascogenous hyphae and fusing ascogonial cells, and their morphological equivalents in the red algae. They illustrate different modes of increase of spore output by splitting up of the oögonium.

NOTE II

The fundamental difference in the method of development of ascospores and carpospores is one of the great barriers in the

way of the descent of the *Ascomycetes* from the *Florideae*. Some (Bessey, E., '13, p. 151) have attempted to overcome this difficulty by suggesting the homology of the ascus and tetrasporangium. But this effort leads to so many suppositions and supporting hypotheses because of the fundamental difference between the process of spore formation in the ascus, and the processes of carpospore or tetraspore formation, that the descent of the ascus fungi from the red algae would require a far more labyrinthian course than would be necessary in deriving them from the *Phycomycetes*.

NOTE III

IS NUCLEAR FUSION IN THE ASCUS OF A VEGETATIVE OR SEXUAL NATURE?

It is unfortunate that there is such great divergence of opinion in the interpretation of the nuclear phenomena in the archicarp and ascogenous threads. These conflicting results are probably, in a large measure, due to the difficulties presented in the minute size of the nuclei. The divergence of opinion relates primarily to the question as to whether the fusion nucleus of the ascus is the result of two successive nuclear fusions, the first taking place in the ascogonium and the second in the ascus, or whether the nuclear fusion in the ascus is the only one.

The principle of a single nuclear fusion, that in the ascus, interprets this act as the final stage in the process of fertilization, by the fusion of two nuclei of more or less remote ancestry. At some time prior to ascus formation these two nuclei may possibly become associated in pairs into a synkarion and multiply in the ascogenous threads by conjugate division, or the synkarion and conjugate division may be postponed to the ascus hook and the complicated series of fusions between the ultimate and antepenult cells of the crozier, or proliferations of the young ascus with accompanying conjugate divisions of the synkarion.

Dangeard ('94) first described the presence of two nuclei in the young ascus, and their fusion, in several species (*Borreria ciliaris*, *Peziza vesiculosa*, *Helvella ephippium*, *Geoglossum*

hirsutum, *Acetabula calyx*, *Exoascus deformans*, and some lichens). The origin of the ascus was correctly described in a number of cases, but in the majority of cases at that time he thought the young ascus arose by the copulation of two unicellular gametes according to a method similar to the formation



Fig. 8. *Pyronema confluens*: A, section of mature discocarp; B, group of archicarps copulating with antheridia by means of the slender prolongation (trichogyne) of the ascogonium which is separated as a distinct cell; C, pair of sexual organs copulating by means of the trichogyne cell, ascogonium at left, antheridium at right; D, showing multinucleate condition of sexual organs and communication of antheridium and trichogyne. a, antheridium; b, trichogyne; c, ascogonium. E, older stage of a similar group of sexual organs after the antheridial nuclei have entered the ascogonium and the trichogyne nuclei have degenerated; also showing early stage of growth of ascogenous hyphae from the ascogonium; F, showing relation of ascogonia, ascogenous hyphae, asci, and paraphyses in mature fruit body.—After Harper.

of the ascus in *Eremascus*, so that the ascus appeared to be supported on two stalks. Frequently, however, in *Peziza vesiculosa* and *Helvella ephippium* he observed the origin of the ascus from a single hypha curving at the end in the form of a hook or crozier. The four nuclei resulting from the division of two were so situated in the crozier that after the formation of two cross walls the ultimate and antepenult cells each contained one nucleus, while the penult cell contained two nuclei. The association of two nuclei in the young ascus and their fusion he interpreted as a sexual act, and the young ascus was looked upon as an oögonium. Later, Dangeard found that the crozier method of ascus formation was the usual one in the forms studied and that in no case in these higher forms did the ascus arise immediately from the conjugation of two different hyphae.

This important pioneer work by Dangeard was a great stimulus to further studies which has led to a more or less clear knowledge of the history of the nuclei from the archicarp through the ascogenous hyphae to the ascus, while the origin of the ascogenous hyphae from the fertile cells of the archicarp was first described by Janczewski ('71) in *Ascobolus*, and later by Kihlman ('83) in *Pyronema confluens*. Harper first demonstrated the origin of the ancestral ascus nuclei in the archicarp of *Sphaerotheca castagnei* ('95^a) and *Pyronema confluens* ('00) and their migration in the ascogenous hyphae, though he does not give the nuclear history in the ascogenous hyphae, except the later stages at the time of formation of the ascus. Their archicarp origin has been abundantly confirmed by several investigators in a number of different forms, both among the lichens and other *Ascomycetes*.

The different opinions in regard to the significance of nuclear fusion in the ascus rest upon the interpretation by different investigators of the behavior of the nuclei in the archicarp, or ascogenous cells, before they begin to move into the ascogenous hyphae. Some maintain that there is a fusion, in pairs, of the sex nuclei (1) in the archicarp when fertilized

by an antheridium (Harper in *Sphaerotheca castagnei*,¹ '95^a, '96; *Erysiphe*, '96; *Pyronema confluens*, '00; *Phyllactinia*, '05; Blackman and Fraser in *Sphaerotheca*, '05; Claussen in *Boudiera* [= *Ascodesmis*], '05); or (2) in the archicarp where the antheridium is functionless or absent (Blackman and Fraser, '06, in *Humaria granulata*; Fraser, '07, in *Lachnea stercorea*). In *Aspergillus herbariorum* Miss Fraser ('07, p. 420) finds that the antheridium often degenerates and did not observe disappearance of the intervening wall when fusion with the trichogyne took place. She *nowhere* describes or figures fusion in pairs of the ascogonial nuclei. She merely assumes it, for, in the summary ('07, p. 428) she says: "It seems probable that normal fertilization occurs in some cases, and that in others it is replaced by a fusion of ascogonial nuclei in pairs"; Welsford ('07) in *Ascobolus furfuraceus*; Dale ('09) in *Aspergillus repens*; Cutting ('09) in *Ascophanus carneus* believe in the fusion of archicarp nuclei in pairs; or (3) of nuclei in vegetative cells where the archicarp is wanting or functionless (Fraser, '07, '08, in *Humaria rutilans*, fusion of the nuclei said to take place soon after entering the ascogenous hyphae; Caruthers, '11, in *Helvella crispa*; Blackman and Welsford, '12, merely found evidence of nuclear fusion in vegetative cells of *Polystigma rubrum*).

¹ Dangeard ('97) claims that the antheridium is functionless and that the single nucleus in the oögonium divides into two. After his study of *Pyronema* Claussen ('12) is inclined to question the fusion of the two sex nuclei in the oögonium of *Sphaerotheca*, *Erysiphe*, *Phyllactinia*, and *Pyronema* as described by Harper ('95^a, '96, '00, '05), and by Blackman and Fraser ('05) in *Sphaerotheca* as well as in the case of *Boudiera* (= *Ascodesmis*) studied by him in 1905. In respect to his work on *Boudiera* he now says: "My own statements upon the nuclear fusion in the ascogone of *Boudiera* (*Ascodesmis*) are clearly wrong." He points out that in none of these cases is the history of the nuclei in the ascogenous hyphae known, and thinks that a reinvestigation will show paired nuclei here. A question to be considered, says Strasburger ('05, p. 24), is whether the chromosomes of the nuclei united in the oögonium do not remain in separated groups in the ascogenous hyphae, in order to fuse as individual nuclei in the ascus. Lotsy ('07) has expressed a somewhat similar view in an attempt to harmonize the situation in the *Ascomycetes* and *Basidiomycetes*. The fusion nucleus in the oögonium remains for a time a 2x nucleus but some time prior to ascus formation the 2x nucleus separates into two individual 1x nuclei in the ascogenous hypha, forming a synkarion. Conjugate division now takes place with ascus formation occurring immediately or after several successive conjugate divisions.

Others maintain with equal assurance that there is no fusion of the sexual nuclei in the archicarp. There is merely an association of sex nuclei.

(1). In forms with a functional antheridium and archicarp may be mentioned *Monascus*¹ (Schikorra, '09) and *Pyronema confluens* (Claussen, '07, '12).

(2). In forms where the antheridium is absent or functionless may be mentioned *Pyronema confluens* (Brown, W. H., '09, antheridium functionless), *Lachnea scutellata* (Brown, W. H., '11, antheridium absent). In both of these examples, cases of division of the nuclei in the ascogonium were observed which might be mistaken for fusion. Since no divisions of nuclei in the ascogonium have been described by authors in the forms where they believe sexual fusions of nuclei to take place, W. H. Brown ('11) suggests that they may have had before them division stages. In

Ascophanus carneus and *Ascobolus immersus* the antheridium is absent, but association of the nuclei in several of the multinucleate ascogonial cells occurs after pore formation in the walls. Most of these nuclei become paired and remain paired as they migrate in the ascogenous hyphae to the ascus hooks, where conjugate division takes place. The only fusion of nuclei is that in the ascus, except in badly fixed preparations or in degenerating nuclei in the ascogonium (Ramlow, '14). In *Leotia* (Brown, W. H., '10) the ascogenous hyphae



Fig. 9. *Pyronema confluens*: A, B, and C, conjugate division of nuclear pairs in the ascogenous hyphae; D, conjugate division in ascus hook; E, tips of branched ascogenous hyphae with ascus hooks, young asci, and beginning of conjugation of the ultimate and antepenult cells of the ascus hooks; F, completed conjugation of the ultimate and antepenult cells of the hook and association of their nuclei as a pair. Ascog., ascogonium; asc. h., ascogenous hyphae with paired "sexual" nuclei.—After Claussen.

¹ Barker ('03) ascribed his failure to find a fusion of nuclei in the ascogonium of *Monascus* to the absence of proper stages in his material.

are supposed to arise from an ascogonium in the base of the ascocarp, but the nuclei are believed to arise from a haploid nucleus. Conjugate division occurs in the ascus hooks, the majority of which are formed by proliferation of the binucleate penult cell and from fusions of the ultimate and antepenult cells of croziers, so that many conjugate divisions of the haploid nuclei take place, and the first nuclear fusion is in the ascus. In *Laboulbenia chaetophora* and *L. Gyrinidarum* (Faull, '11, '12) fusion of nuclei does not occur in the ascogonium, the mature binucleate ascogenic cell develops the asci by budding, each ascus bud being preceded by a conjugate division of the nuclear pair. In *Polystigma rubrum* (Nienburg, '14) no fusion in the ascogonium occurs. In *Collema pulposum* (Bachmann, '13) the nuclei in the ascogenic cells were often found in pairs, but no cases of fusion were observed.

(3). Forms in which an archicarp is absent or functionless, and certain vegetative cells take on the function of ascogenic cells, in which the authors believe nuclear fusion does not take place except in the ascus: *Gnomonia erythrostoma* (Brooks, '10); *Helvella elastica* (McCubbin, '10) in which the "ascogenous hyphae" form an intricately interwoven subhymental layer of threads each with two nuclei in the end. The ends of these hyphae form croziers with conjugate division of the two nuclei followed by about six repeated proliferations of the young ascus and crozier formations, accompanied by fusions of the ultimate and antepenult cells and crozier formation, resulting in many successive conjugate divisions of the haploid nuclei, with fusion first in the ascus. In *Xylaria tentaculata* (Brown, H. B., '13) the ascogenic cells which appear to be derived by the separation of the cells of "Woronin's hypha" are uninucleate and soon become multinucleate by nuclear division. The nuclei multiply also in the ascogenous hyphae.

The theory of a vegetative fusion in the ascus arose from the belief on the part of some students that sexual fusion of the nuclei occurred in the ascogonium, that the nuclear fusion in the ascus must be a second fusion with no relation to the

sexual process, and, therefore, it must be of a vegetative nature. If a second fusion of the nuclei occurred it would call for a triple division of the fusion nucleus in order that the haploid condition should be again reached.

The universal occurrence of the triple division in the ascus in the formation of the spores is by some ascribed to a "quadrivalent character" of the chromosomes in the fusion nucleus, and rendered necessary in the return to the univalent condition (Harper, '05; Overton, '06), and Overton states, "that all these divisions persist, no matter how many spores are to be produced, which shows their necessity in the process of reduction."¹ *Eremascus* controverts this statement since there is certainly but one fusion (Stoppel, '07; Guilliermond, '09) and yet triple division occurs in the ascus.

The results of cytological investigations by different students in connection with the triple division show considerable variation. Thus Harper ('00, '05) finds the same number of chromosomes in all three divisions (10 in *Pyronema*, 8 in *Phyllactinia*). The two ascus nuclei "fuse with all their corresponding parts" (Harper, '05, p. 67), so that the quadrivalent nature of the chromosomes in the fusion nucleus is not to be seen, though he conceives it to exist. Synapsis occurs in the first division.

Miss Fraser ('07, '08) describes *Humaria rutilans* as having 16 chromosomes in the first division where synapsis occurs (heterotypic) which split transversely and the daughter nuclei have each 16 chromosomes which appear on the nuclear plate in the second division. In the second division the chromosomes split longitudinally (homöotypic) and 16 chromosomes pass to each daughter nucleus. In the third division the 16 chromosomes are supposed to separate at the nuclear plate without division, 8 going to each daughter nucleus. This division she terms "brachymeiotic". A similar situation is described by Fraser and Welsford ('08), Fraser and Brooks ('09), and Carruthers ('11). Faull ('05) finds the same num-

¹ Polysporous asci resulting from several to many nuclear divisions may be the retention of an ancestral character, the number of divisions being reduced to three in most forms.

ber of chromosomes in all three divisions, in some species 4 or 5 (*Hydnobolites*), in others 8 (*Neotiella*).

More recently Claussen ('12) after a very thorough study of *Pyronema confluens* finds the same number of chromosomes (about 12) in all three divisions. The first division is heterotypic accompanied by synapsis, diakinesis and a splitting of the chromosomes. The second is homöotypic, while the third is typic. Faull ('12) in a recent study on *Laboulbenia* also finds that the two first divisions in the ascus agree with the usual phenomena accompanying reduction in spore mother cells, the first being heterotypic, while the second follows "very swiftly on the heels of the first." He concludes that "probably the only nuclear fusion in the life cycle is that in the ascus," and that conjugate divisions of nuclei are an important phase in the sexual phenomena of the *Ascomycetes*.

The evidence from recent investigations, therefore, supports more and more the interpretation of nuclear fusion in the ascus as a process of exactly the same significance as the nuclear fusion in the basidium of the *Basidiomycetes*, and in the teleutospore of the *Uredinales*, i. e., it is the fusion of a pair of nuclei of a longer or shorter history of conjugate divisions from a pair of ancestral nuclei of more or less remote association. This association of nuclei arises in a variety of ways and at different periods in the ontogeny just as it does in the *Basidiomycetes* (Maire, '02; Ruhland, '01; Harper, '02; Nichols, S. P., '04; Kniep, '13), and *Uredinales* (Sappin-Trouffy, '96; Maire, '99, '01; Blackman, '04; Christman, '05, '07; Blackman and Fraser, '06; Olive, '08; Hoffmann, '12; Werth und Ludwigs, '12). The association is accomplished in some cases through the copulation of two gametangia (*Pyronema*, *Monascus*, *Gymnoascaceae*, and the *Erysipheae*). Such an association represents nearly, if not quite exactly, the true type of sexuality. The other methods of association represent a variety of modified types of sexuality (see Note 1) where the archicarp is present and the antheridium absent, or functionless, or where the archicarp is absent and vegetative cells, either with or without the migration into them of nuclei

from adjacent vegetative cells, give rise to the ascogenous threads.

The results of recent work tend more and more to show that there is no fusion of the associated nuclei in the ascogonium, or ascogenic cells, whether certain of the nuclei have been derived from an antheridium (*Pyronema*, Claussen, '12; *Monascus*, Schikorra, '09), or not. Conjugate division in the ascogenous threads has been abundantly proven, though in some cases it may occur only one or a few divisions prior to the formation of the ascus.

What the peculiar features of nuclear fusion in the ascus are which characterize it as vegetative, seem to rest more on an *ex parte* judgment of a fusion of nuclei in the ascogonium than upon any well established idea of the nature of vegetative nuclear fusion. Thus, Miss Fraser ('08, p. 37) states that in *Humaria rutilans* the two nuclei in the ascus enter independently upon the prophase of the first division, fusing in the spirem stage. This she regards as evidence in disproof of the sexual nature of the fusion of nuclei in the ascus ('08, p. 44). Harper ('05) raises a similar objection. On the other hand, it seems to me that it is excellent evidence that it is not of a vegetative nature. It is well known in a number of cases that the egg and sperm nuclei, lying side by side in the egg, undergo the prophase stages of division up to the formation of the chromosomes before fusion of the two takes place. I cite certain examples in the *Abietineae*: *Pinus sylvestris* (Blackman, '98); *P. strobus* (Miss Ferguson, '01, '04); *Tsuga canadensis* (Murrill, '00).

In support also of the supposed vegetative nature of the fusions in the ascus Miss Fraser ('13, p. 559) cites "vegetative nuclear fusions" in the quadrinucleate ascus of *Humaria rutilans* and her work on this plant in 1908. But she nowhere describes or figures the fusion of the four nuclei in such asci. She says ('08, p. 41) "trinucleate (Fig. 50) and quadrinucleate (Fig. 51) asci are sometimes formed; their fate could not be determined." It is very likely that such tetranucleate young asci found by Miss Fraser in *Humaria* result from further conjugate division prior to the prolifera-

tion of the young ascus to form branches and further croziers resulting in an increase of asci as shown to take place in *Pyronema confluens* by Claussen ('12, p. 25, fig. 6, III).

It has been suggested by some who regard the fusion in the ascus as a second fusion of nuclei (Harper, '05; Overton, '06) that if the synkaryophytic condition of the terminal portion of the ascogenous hyphae in *Pyronema*, and far back in those of *Galactinia succosa* (Maire, '03, '05), could "work back until the egg cell was reached," an apogamous condition might result similar to that in the *Hymenomycetes*. Certainly those who have suggested this theory have not thought far enough ahead, for how would the univalent condition of the spore nucleus pass to the bivalent condition of each nucleus prior to the paired (= quadrivalent) condition in the ascogenous hyphae of the next generation unless this were preceded by a nuclear fusion. Such a condition would not be apogamy. The quadrivalent character of the fusion nucleus of the ascus, or of the synkarion in the ascogenous threads, demands two successive nuclear fusions, if the triple division in the ascus brings about the reduction of a quadrivalent nucleus to a univalent one as maintained by the adherents of this theory. As to such an apogamous condition being similar to that in the *Hymenomycetes* it must be remembered that there are only two divisions in the reduction process in the *Hymenomycetes*, so that when two univalent nuclei become associated in cells of the mycelium or basidiocarp the bivalent condition of these cells is attained.

In a very interesting and scholarly argument Harper ('05) has attempted to explain the inclusion and fusion of two nuclei in the young ascus on the basis of the nucleo-cytoplasmic relation or balance in the cell. The abundance of food material in the tips of the ascogenous hyphae inhibits cell wall formation so that two nuclei are enclosed in one cell. Rapid growth of the ascus and cytoplasm follows in order to balance the relation of the latter with the nuclear mass. The fusion of the nuclei and growth of the fusion nucleus again overbalance the cytoplasm, which then by growth increases again

in mass. The process is thus a reversible one, and by a sort of see-saw growth of nucleus and cytoplasm the ascus cell is pushed up to the large size characteristic of spore mother cells.

It is very true that the "regulative function is a reversible one," that an active cell with a large amount of cytoplasm demands a correlative amount of nuclear substance, that the increase in one may result in the increase of the other. Also it is very true that the ascus belongs to the category of spore mother cells, which are characterized by relatively large nuclei and cytoplasmic mass compared with most vegetative cells, but this does not explain why, when ascus or spore mother cell formation is about to take place, cell division does not occur at a period when the food relation would permit the formation of young uninucleate asci if these nuclei are bivalent in nature. The regulative functions accompanying growth and maturity of such a young gonotokont would assure sufficient size, sufficient food material, and the necessary equilibrium. The fact that asci in different species and groups vary so greatly in size shows this, and also that there is no general standard of mass in relation to surface area which would demand two nuclei at the origin of the ascus.

In fact it is very clear, from the morphological processes which take place in the tip of the ascogenous hyphae of most of the forms studied, that cell division, or cell wall formation, is more likely governed by the last division of the two nuclei so that the cell walls are laid down between the daughter nuclei. If the inclusion and fusion of two nuclei in the young ascus were controlled entirely by nutritive and cyto-regulative processes, why are not sister nuclei included? Surely the purely cyto-regulative functions would be just as well satisfied. It appears that in rare cases sister nuclei may be included in the ascus (Brown, W. H., '10, in *Leotia chlorocephala*).

Of the four nuclei resulting from the two successive divisions of the zygote nucleus in *Spirogyra*, Chmielewski ('90) states that two fuse to form the nucleus of the single germling which is usually formed in the *Zygnemaceae*. Harper inter-

prets this as a vegetative fusion in support of his interpretation of vegetative fusion in the ascus. Karsten ('08) describes the divisions of the zygote nucleus into four nuclei in *Spirogyra jugalis*, but does not state the relation of the nuclei to the germling (second division sometimes omitted). Tröndle ('07) interprets the process in *Spirogyra Spréeiana* as presenting but a single division of the zygote nucleus. Results of this nature, so divergent from expectations based on the normal history in many other organisms in widely separated groups, are usually received with considerable reserve, particularly where they are pioneer investigations in a group not yet studied. Recently Kurssanow ('11) in a thorough study of nuclear division and germination of the zygote in two species of *Zygnema* (*Z. cruciatum* and *Z. stellinum*) has shown that the process is normal, there being two successive divisions, three of the nuclei usually degenerating, while one becomes the nucleus for the single germling characteristic of the *Zygnemaceae*. Occasionally only two of the nuclei degenerated, but then two germlings were formed, an interesting case showing a tendency to retain what is believed to be the ancestral condition where four germlings are formed as in the *Mesotaeniaceae*, while in the desmids two germlings are regularly formed.

Other cases cited as examples of vegetative nuclear fusion and classed with nuclear fusion in the ascus, are those of the endosperm nucleus with the second sperm nucleus in seed plants (Harper, '05), and (Fraser, '13) nuclear fusions in paraphyses and in hairs of the excipulum of certain discomycetes. Such cases, however, cannot be legitimately compared to fusion in the ascus, since those nuclei are shut off from further participation in the line of successive ontogenies.

The example cited by Harper of Boveri's ('88) experiment in shaking sea urchin's eggs after fertilization, resulting in the production of an abnormally large larva with 72 instead of 36 chromosomes, is in a different class from most of the other examples of vegetative fusion given. This is equivalent to a true double fertilization and it is quite within the bounds of possibility that among many such larvae some

might under favorable conditions be the starting point of a new ontogeny which would be similar to certain mutants. The case of *Oenothera gigas* (see De Vries, '03, '13) a mutant from *Oe. Lamarckiana* with double the number of chromosomes is similar.¹ Other tetraploid mutants are known (see Gates, '13), the diploid gametophyte and tetraploid sporophyte of the mosses produced experimentally by Marchal ('09, '11) is interesting in this connection.

Now, the possibility of a similar double fertilization in an ascomycete is not, a priori, excluded. There might be an isolated example. But the normal expectation is that it would have afterward a nuclear history in its ontogeny similar to others with one nuclear fusion and one reduction from $2x$ to $1x$. But it is not likely that the entire group of sac fungi is founded on such a mutation, followed by a double reduction with triple division and then double fertilization again and so on. The several cases where it has been quite well established that there is no nuclear fusion prior to the ascus, together with the great uniformity of the ascus nuclear phenomena in the group, controverts the idea of any such origin for the sac fungi.

All of these facts go to prove that the inclusion and fusion of two nuclei in the young ascus is of a very different and far greater significance than a vegetative one. The process of nuclear fusion in the ascus does not comprise in itself the entire series of events generally accepted as belonging to the process of fertilization, for in most organisms nuclear fusion occurs in the same cell where nuclear association takes place. It is generally conceded that before the haploid condition of the nucleus is again established important processes take place which we call reduction phenomena, the full significance of which we perhaps are as yet ignorant of. These processes, including synapsis, cannot take place unless nuclear fusion has occurred, and some students see in

¹ Just how the doubling arose in this instance is of course difficult to determine. Stomps ('12) suggested that it arose through the union of two unreduced diploid gametes, while Gates ('09, '13) thinks it arose through "suspended mitosis of a megaspore mother cell" having ($4x$) 28 chromosomes, and its apogamous development.

them the real act of fertilization (Strasburger, '00, '04, '05).

Remarks on the origin of the specialized ascus.—In the direction of progression from the generalized ascus by splitting up of the zygote, the diploid phase has been prolonged and the number of spores multiplied. The filamentous outgrowths of the zygote, or its equivalent, provide numerous terminal cells of restricted size suitable for the production of a small number of spores in each, following the meiotic divisions of the fusion nucleus which terminate the diploid phase.

The situation in species with polysporic asci, where the spores result from numerous divisions of the fusion nucleus, is interpreted by some as a germination phenomenon (Overton, '06), but it seems to me more comprehensible to regard it as a retention of a primitive feature existing in certain phycomycetous ancestors, and characteristic also of primitive *Ascomycetes* like *Dipodascus*.

The formation of internal non-motile spores through free cell formation in the zygote, under conditions adapted for dispersion by ejection from either the generalized or specialized ascus, may be sufficient to account for the distinctive processes of spore formation in the sac fungi. In the oögonium of *Saprolegnia*, functional nuclei in the oögonium are very similar to the nuclei of the ascus preceding ascospore formation. The nucleus is provided with a prominent central body at its pointed end from which kinoplasmic radiations extend (Hartog, '95; Claussen, '08; Mücke, '08).

In most of the *Ascomycetes* the cytoplasm in the ascus is differentiated into epiplasm and spore plasm, the former assisting in the ejection of the ascospores. This separation of the plasm may have been one of the direct causes of the peculiar method of ascospore formation.

NOTE IV

THE PHYLOGENETIC RELATION OF THE TRICHOGYNE AND SEXUAL APPARATUS OF THE ASCOMYCETES AND THOSE OF THE RED ALGAE

The sexual apparatus of the *Ascomycetes*, particularly the trichogyne and the so-called spermatia, is generally conceded to be the strongest evidence in support of their phylogenetic

relation to the red algae. The analogy at least between the trichogyne of the red algae and that of the *Ascomycetes* is very striking. The evidence brought forward by Stahl ('77) and others of the relation of the trichogyne to the ascogonium in the lichens, together with the fusion of spermatia to the trichogyne, followed by the gradual and peculiar degeneration of the latter and the subsequent development of the ascogenous threads, was generally accepted as proof of fertilization in the ascogonium by a spermatium. Also the early studies of *Polystigma rubrum* (Fisch, '82; Frank, '83) and *Gnomonia erythrostoma* (Frank, '86) in which similar structures and phenomena were observed at that time, were generally accepted as indicating a well developed condition of sexuality. These studies gave a great impetus to the theory suggested by Sachs ('96) that the *Ascomycetes* had their origin from the red algae, or that the two groups had ancestors in common. This theory has taken very deep root and probably is accepted by a majority of botanists even at the present time, especially by those who are not special students of the fungi. It should be stated also that a number of our foremost students of the fungi, perhaps a majority of them, are firm disciples of this theory.

Recent investigation, however, including a cytological study of several of the now classic types, including *Collema* (Bachmann, Miss F. M., '12, '13), *Polystigma rubrum* (Blackman and Welsford, '12; Nienburg, '14), *Gnomonia erythrostoma* (Brooks, '10) have failed to furnish any evidence of a real sexual function on the part of either the trichogyne or spermatia in any of the species of fungi possessing these two structures. Pairing of nuclei in the oögonium, or the pairing of these with nuclei from adjacent cells of the ascogonial branch or archicarp, furnish the synkaria, or the synkaria are organized at different stages in the development of the ascogenous hyphae (see Note III). In some quarters these results have led to a loss of confidence in the sexual significance of the trichogyne and spermatia of the *Ascomycetes*. Some have therefore attributed to the trichogyne a physiological significance of another kind, that of a respiratory organ for

example (Brooks, '10), or a boring organ, a terebrator (Lindau, '99). Zukal ('89) interpreted the trichogyne of *Pyronema confluens* as a haustorium to provide food for the large ascogonium with its numerous ascogenous threads.

Recent investigations on *Collema pulposum* (Bachmann, F. M., '13) have revealed an interesting departure in the relation of the trichogyne and spermatia from that thus far found in other lichens, and is in strong contrast with the condition found by Stahl in *Collema*. The "spermatia" are not free and are not formed in large numbers in superficial receptacles, but are imbedded in the thallus and remain attached to the supporting hypha. The trichogyne does not extend to the surface but migrates through the interior of the thallus, seeks the spermatia and fuses with one. Then the trichogyne undergoes the usual deterioration, but no evidence was obtained of the migration of the nucleus of a spermatium to the ascogonium, although a nucleus supposed to be the sperm nucleus appears to have been observed in the terminal cell of the trichogyne.

In the red algae the only variations and progression in the trichogyne is in variations in length to meet the requirements of thin or thick cortex, some more or less sinuous or spirally wound, and a few stout and blunt. It is universally a continuous, enucleate,¹ prolongation of the oögone, i. e., not septate nor a separate cell. So far as we know the sperm always functions in the red algae. In the sac fungi, there is great variation and marked morphological progression from an oögone without a trichogyne through short one-septate trichogynes to long, simple, several-celled ones, and also to profusely branched, multi-septate trichogynes. It is more comprehensible to regard this progression and variation in the light of evolution from the simple to the complex, in the ascomycete phylum, independent of the red algae, than to con-

¹ Davis ('96) describes the trichogyne of *Batrachospermum* as having a nucleus of its own, but it is not separated from the egg nucleus by a wall until just prior to the development of the gonimoblasts from the egg. He also states that the sperm nucleus never passes out of the trichogyne into the egg. However, Schmidle ('99) and Osterhout ('00) find no trichogyne nucleus and describe a real fertilization by fusion of sperm and egg nucleus.

ceive the long septate trichogyne of the highly specialized *Collema* to be derived directly from the simple trichogyne of the red algae, and then degenerate to the simple gamete of lower more generalized *Ascomycetes*.

NOTE V

MODIFICATION OF SEXUAL PROCESS ALONG WITH STERILITY OR LOSS OF THE
ANTHERIDIUM AND STERILIZATION OF THE ARCHICARP

Sterility or loss of the antheridium.—Several species are known in which the antheridium, though present, does not function. In such cases sexuality is modified in such a way that sex differentiation occurs among the nuclei in the ascogonium or in the ascogenous hyphae. Several examples may be cited as follows: In *Pyronema confluens* (Brown, W. H., '09) the antheridium sometimes fuses with the trichogyne but there is no migration of its nuclei; in other cases it may not connect with the trichogyne. The antheridial nuclei degenerate. In still other cases the antheridium is absent. In *Lachnea stercorea* the antheridium fuses with the terminal cell of the archicarp but its nuclei degenerate (Fraser, '07). In *Aspergillus herbariorum* (Fraser and Chambers, '07) and *A. repens* (Dale, '09) a similar situation exists. In those numerous examples where spermatia (mostly free "antheridia") are present it is very likely that the sperm nuclei no longer play a rôle in fecundation due to such extensive sterilization of the terminal segments of the archicarp, but the cytology of only a few species has been determined. They no longer perform the function of fecundation in *Polystigma rubrum* (Blackman and Welsford, '12; Nienburg, '14), *Gnomonia erythrostoma* (Brooks, '10), and in *Collema pulposum* (Bachmann, '13) the sperm nucleus has not been traced through the long succession of sterile segments of the archicarp, and it is very probable that it does not reach the ascogonial cells. The spermatia are entirely absent in a number of species where archicarps are present, as in *Laboulbenia chaetophora* (Thaxter, '96; Faull, '12).

Sterilization of the terminal portion of the archicarp and differentiation of sex nuclei in the ascogonium or ascogenous

hyphae.—A moderately large number of species, in which more or less extensive sterilization of the terminal portion of the archicarp has occurred, have been examined by cytological methods and in most cases a reduced or modified sexual condition has been found.

In *Pyronema confluens* great variations occur in the sexual nature of the ascogonium. In what may be called normal cases, antheridial nuclei enter and become associated with the ascogonial nuclei (Harper, '00; Claussen, '07, '12). Under cultural conditions the antheridium may be normal, rudimentary or absent, but the ascogonium develops in a normal manner (van Tieghem, '84). Different strains may also behave differently. In some the antheridium does not fuse with the trichogyne, while in others it does (Brown, W. H., '09). In some cases even when the antheridium fuses with the trichogyne, its nuclei do not pass into the ascogonium (Dangeard, '07), but degenerate *in situ* (Brown, W. H., '09). In these cases where the antheridium does not function the sexuality of the ascogonium is modified in as much as its nuclei are differentiated sooner or later so that in pairs they perform the function of sperm and egg nuclei. According to W. H. Brown ('09) in cases where the origin of the pair of nuclei in the ascus hook could be determined, they were sisters. After the one conjugate division in the hook the two nuclei in the ascus, or penult cell, are "cousin" nuclei.

The archicarp of *Lachnea scutellata* (Woronin, '66; Brown, W. H., '11) consists of about nine cells. No antheridial structure has been observed. The penultimate cell functions as the ascogonium (Brown, W. H., '11). It is multinucleate and no fusion of nuclei in pairs takes place here. The nuclei are increased in numbers by division, not only in the ascogenous threads where they do not appear to be paired or show conjugate division, but also in the ascus hook where conjugate division takes place. The numerous fusions of the terminal and basal cells of the ascus hook result in numerous successive conjugate divisions. In *Leotia*, although the archicarp has not been clearly observed, it would appear from the account (Brown, W. H., '10) that the antheridium is absent (or

if present, functionless) and that the ascogonium consists of a single coenocytic cell. Conjugate division takes place in the ascus hook, and the subsequently fusing cells, so that in most cases rather distantly related pairs of nuclei form the fusion nucleus in the ascus. In *L. chlorocephala* (Brown, W. H., '10), it appears that the pair of ascus nuclei are sometimes sisters. This would indicate an extreme case in the modification of sexuality, the distance of relationship between the sex nuclei being reduced to the minimum. It recalls the very close relationship of the sex nuclei in many of the lower algae, particularly in certain diatoms¹ (Oltmanns, '04), and in the species of *Spirogyra* having buckle-joint conjugation (Chodat, '10). In the case of *Spirogyra* it is not known whether the pair of sex nuclei in this type of conjugation are cousins or sisters, or whether now one and then another of these possibilities exists. Such species of *Spirogyra* in which certain threads present scalariform as well as buckle-joint conjugation offer an interesting parallel to the variation in distant relationship of the fusing nuclei in the young ascus.

In some other species where the antheridium is functionless or wanting, sex differentiation is said to take place among the nuclei in the ascogonium. This indicates a sex differentiation much earlier than that which is supposed to occur in the species just cited. This differentiation in sex nuclei has been described in *Humaria granulata* (Blackman and Fraser, '06).

Another species in which similar phenomena are described is *Lachnea stercorea* (Fraser, '07). Here the archicarp consists of several coenocytic large cells and the terminal trichogyne of 4-6 smaller coenocytic cells. The unicellular coenocytic antheridium fuses with the terminal cell of the trichogyne, but its nuclei do not reach the single-celled ascogonium, among whose nuclei sex differentiation is said to take place.

For a number of years *Polystigma rubrum*, a parasite on cherry leaves, as the result of studies by Fisch ('82) was regarded as an example of fertilization of an ascogone coil by

¹ In *Achnanthes subsessilis*, the protoplast divides into two parts along with nuclear division. The two uninucleate protoplasts now immediately unite in auxospore formation.

sperm nuclei from spermatia after passing through a long succession of cells constituting the trichogyne or sterile portion of the archicarp. The trichogyne, or sterile portion of the archicarp, is very long and branches into two portions, one extending to either surface of the leaf. But according to Nienburg ('14) sex differentiation has occurred between the basal cells of the archicarp and a nucleus from the basal cell migrates into the adjacent cell, which becomes the ascogonium or ascogenic cell, but nuclear fusion does not take place here.

Loss of function by the archicarp or its disappearance.—A number of examples are known in which the archicarp has either lost its function as a sexual organ or ascogone, or has disappeared. In such cases differentiation of sex occurs in special vegetative cells, sometimes by the migration of a nucleus from certain cells into adjacent ones. In *Gnomonia erythrostoma*, although Frank ('86) described coiled ascogone-like structures with trichogynes, and believed that the coils were fertilized through the agency of the spermatia, recent cytological work (Brooks, '10) on this species appears to show that the tufts of hair-like structures emerging through the stomates of cherry leaves, on which this species of *Gnomonia* is parasitic, are not now connected with the coiled hyphae deeper in the tissue. It appears also from the same work that the ascogenous hyphae do not arise from the coils, but from one or more slightly differentiated hyphae in the center of each coil.

A similar example is found in *Xylaria polymorpha* (Fisch, '82), where an extensively coiled hypha ("Woronin's hypha") occurs in the early stages of the formation of the ascocarp, but later disappears and certain vegetative cells give rise to the ascogenous hyphae.

In *Humaria rutilans* (Fraser, '08) no archicarp or ascogone coil is discernible, but certain vegetative cells function as ascogenic cells following the migration into them of nuclei from adjacent cells.

MORPHOLOGY OF THE ARCHICARP

If the history of the *Ascomycetes* is correctly read from the simpler and more generalized forms to the complex and

highly specialized ones as Sachs ('74, '96), de Bary ('81, '84), and many other students have advocated, the female organ or archicarp first appeared as a "unicellular" or continuous organ, not differentiated into an oogonium or fertile portion, and a trichogyne. The presence of a "procarp," whether consisting of one or several cells, which ultimately gave rise to the asci or ascogenous threads was the predominant character which led Sachs in 1896 to believe in the phyletic relation of the sac fungi and red algae, although earlier he had regarded the morphology of the ascocarp and cystocarp of greater importance in showing relationship. No known red alga possesses a procarp simple enough to represent the prototype of the two groups. *Gymnoascus* was selected by Sachs as representing the simplest *Ascomycetes*. The archicarp of *Gymnoascus* is a continuous structure more or less coiled around the antheridium from which it copulates directly without the intervention of a trichogyne.

After copulation the ascogonium divides into several cells which give rise to the ascogenous hyphae. In some forms the splitting up of the ascogonium by transverse division occurs at an earlier period, before copulation. There is some evidence which indicates that the "trichogyne" in the *Ascomycetes* primarily was a prolongation of the "unicellular" oogone (or carpogone), and that when it was first separated as a distinct cell it was still a fertile part of the archicarp. In *Aspergillus repens* the terminal cell, or "trichogyne," sometimes gives rise to ascogenous hyphae (Fraser, '08).

The terminal cell became merely a trichogyne when it ceased to give rise to ascogenous hyphae, and acted as a transport tube for the sperm nuclei from the antheridium to the ascogonium, as in *Pyronema* and *Monascus*. The septum between the terminal cell and the functional ascogonium was an impediment to the passage of the sperm nuclei, as well as the fact that when they entered the terminal cell of the archicarp they did not meet with functional egg nuclei. This situation very likely favored the assumption of sperm and egg functions by the nuclei of the functional ascogonial cell. The variations in *Pyronema* where the antheridium may or may

not be present, and often when present and fused with the trichogyne its nuclei degenerate and the ascogonium is still functional producing ascogenous hyphae and asci, is in support of this interpretation.

Further sterilization of the terminal portion of the archicarp proceeds as it becomes longer and more septate, the fertile ascogonial cell or cells being near the center or base. All of the sterile portion of the archicarp distal to the ascogonial cells is usually interpreted as the trichogyne. I believe it would be more in harmony with the historical origin of the archicarp, and with the real homologies, if only the terminal sterile receptive cell of the archicarp were called the trichogyne, the other portions to be regarded as sterile portions of the archicarp or ascogonium. This would be in harmony also with Thaxter's ('96) interpretation of the archicarp of the *Laboulbeniales*.¹ In this group the inferior and superior supporting cells are sterile cells of the archicarp derived by a transverse splitting of the ascogonium. Even with this interpretation of the trichogyne of the *Ascomycetes*, it would be a different structure from that of all the red algae where it is merely a continuous prolongation of the egg cell.

NOTE VI

The coenocytic character of the mycelium of the *Phycomycetes* has been presented as an obstacle to the derivation of the sac fungi from the sporangium fungi (Bessey, E. A., '13); this character can, however, have very little or no significance, for many of the *Ascomycetes* are coenocytic. As in most of the fungi, cell wall formation is delayed so that new portions of filaments are often multinucleate, the cell walls being laid down subsequently, sometimes enclosing one nucleus, sometimes several in a cell. There are the monoenergid and polyenergid species of sac fungi. In the *Phycomycetes* cell wall formation is usually longer delayed or does not occur except where reproductive cells are formed. In the *Mucorales* old mycelium frequently becomes multiseptate. It should be noted that in *Basidiobolus* (Eidam, '86; Raciborski, '96; Fair-

¹ Except in the case of the multiseptate branched trichogynes.

child, '97, and others) the cells are uninucleate. The variation in coenocytic character of mycelium probably is due in some measure to the usually fundamental difference between cross wall formation in dividing cells, in the thallophytes and the higher groups of plants, where the fibers of the inner spindle play a part and the cell wall development is centrifugal, while in most thallophytes the spindle fibers do not play such a part, wall formation being centripetal, like a closing iris diaphragm.

The strong plasma connections between the protoplasts of the *Laboulbeniales* (Thaxter, '96) present a very striking resemblance to those in the red algae. This feature is regarded by some as very strong evidence of a phylogenetic relation between the *Laboulbeniales* and the red algae. But intercellular plasma connections are a common feature in all groups of plants, though in many plants these connections are very minute. The single central pore in the wall of the *Laboulbeniales* is perhaps the result of incomplete closing of the ring-forming wall, and in the *Laboulbeniales* would seem to be of physiological rather than of phylogenetic significance. The firm cell walls which are characteristic of the members of this group bear a very definite relation to their habit as external parasites of insects. Standing out free from their bodies and thus having no other means of support than their own rigidity, thick cross walls would interfere with transport of food material, while the prominent plasma connections permit easy passage of nutrients.

NOTE VII

BRIEF OUTLINE OF SOME OF THE THEORIES AS TO THE PHYLOGENY OF THE ASCOMYCETES

I. *Descent from the Rhodophyceae*.—Sachs ('74, p. 287) regarded the resemblances between cystocarp and ascocarp as the most important character indicating a relationship between the red algae and sac fungi, although the form of the sexual organs, particularly the carpogonial branch, was also believed to point in the same direction. In his 'Lehrbuch der Botanik' he did not even suggest that the *Ascomycetes* were derived from the *Florideae*. The relationships were based

on the principle of morphological homology, which he believed were great enough to justify their inclusion in the same class. To justify his arrangement in one large group of plants with such diverse aspects and habitats, he cites the inclusion of the *Lemnaceae* and palms in the great group of the monocots. We could not then interpret his inclusion of the sac fungi and red algae in one class, the *Carposporeae*, as indicating that the former were derived from the latter.

Sachs says ('74, p. 288) that in order to find the relationships between plant divisions one must compare the simplest, not the highest forms. By this method he finds that the *Coleochaetaceae* and *Characeae* are linked, on one hand to the simplest *Florideae*, and on the other to the simplest *Ascomycetes*. Each of these series, he says, has developed in its own peculiar manner to higher forms, so that if one compared the most complete *Ascomycetes* with the coleochaetes only very slight resemblances are to be found. From this it is very clear that Sachs, at that time, had no thought of the derivation of the *Ascomycetes* from the *Florideae*. There is nothing to indicate that he believed the *Ascomycetes* descended from the charas and simplest coleochaetes, to which he says the simplest *Ascomycetes* are most closely related. Nor would his theory require a common ancestor for the two groups. Because of the morphological resemblance between cystocarp and ascocarp, he would have united the *Ascomycetes* and *Florideae* into a higher group even had he believed that the former were derived from the *Phycomycetes*.

It has been said by Sachs ('96, p. 204) that the fungi as a whole cannot be valued as an architype because, as apochlorates, they must be descended from green plants. The bacteria he would derive from the *Cyanophyceae*, the *Phycomycetes* from the *Siphonaceae*, and the *Ascomycetes* (or at least the *Discomycetes*) from the *Rhodophyceae*. The predominant feature indicating the descent of the sac fungi from the red algae he now sees in the procarp of both groups ('96, p. 205).

The chlorophyllless seed plants have only a slight form-producing power or motive, as Sachs has pointed out ('96, p. 205), since they occur mostly as small plant groups within certain

green leaved families and show very plainly the morphological characters of their antecedents. But he says it is quite otherwise with the fungi. The simplest primitive forms of the *Ascomycetes*, *Phycomycetes* and *Basidiomycetes* have given rise independently to an enormously high state of differentiation. Now Sachs in 1896 (and earlier, '74, p. 310) recognized *Gymnoascus* as belonging to the simplest *Ascomycetes*, the sexual organs of which are a simple carpogone and pollinode. It is very clear then that Sachs would not derive the *Ascomycetes* from any primitive form at all like any known red algae, much less through such forms as the highly specialized *Collema* or *Polystigma*. This warrants us in concluding that Sachs had in mind a primitive hypothetical ancestor of the sac fungi and red algae, which possessed simple copulating gametes. With the knowledge we possess to-day of such forms as *Dipodascus*, *Eremascus*, etc., where the zygote becomes the ascus (generalized or simple) I believe he would have recognized in the *Phycomycetes*, as we know them to-day, a situation very closely approximating an "Urform" for the *Ascomycetes*, particularly in view of the fundamental difference in the cytology of the red algae and sac fungi.

But whether the fungi represent one or several archetypes it by no means follows that, because of the absence of chlorophyll, they *must* be derived from green plants, or that each great series must be derived separately from different groups of algae.

The appearance of the higher fungi (*Eumycetes*) was, in the opinion of Vuillemin ('12, p. 223), contemporaneous with the emergence of sea-shore, which abandoned certain red algae to a terrestrial life. This new environment introduced the change, which, accompanied by loss of chlorophyll, gave rise first to the *Pyrenomycetes*, from which the other higher fungi (*Uredinales*, *Basidiomycetes*) have originated. The saprophytic forms represent the productive and progressive stock. Parasitic groups, like the *Uredinales*, *Laboulbeniales*, lichens, etc., are composed of highly specialized and uniform members, their progressive potentialities being suppressed, but they retain their hold on existence because of their specialized hab-

itat. The first *Pyrenomycetes*, according to his view, were some of these depatriated red algae, losing their pigments while preserving the structure, the sexual organs and the general evolution. But he recognized no known member of the red algae as a prototype of the *Pyrenomycetes*. Primitive trichogyne-bearing algae gave rise to the red algae on one hand, and to the *Pyrenomycetes* on the other, the now known colorless red algae (like *Harveyella mirabilis*, *Choreocolax alba*) being recently reduced forms having no significance in the origin of the sac fungi. But the *Pyrenomycetes* with well developed trichogyne and spermatia are chosen as the primitive forms, the simplest represented by *Polystigma* (in his "*Polystigmatales*") the higher ones (his "*Pyreniales*") giving rise successively to the *Hysteriales* and *Phacidiales*. From the *Polystigmatales* three other lines arose, their simplest forms being represented by first, *Gymnoascus*; second, *Pyronema*; and the third line represented by the *Laboulbeniales* (see Vuillemin, '12, pp. 338-341).

Bessey ('14) regards the *Discolichenes* as the most primitive *Ascomycetes*. This theory is based on the supposed phyletic relation of the multiseptate trichogyne of the lichens (*Collema*, for example) to the trichogyne (a mere tubular, continuous, prolongation of the egg) of the red algae. Certain of the red algae became parasitic on blue-green algae and on simple members of the green algae, forming a lichen thallus. It is supposed that this parasitism may have had its origin while both kinds of organisms still lived in the water, but finally the lichen assumed the land habit. The improbability of such a derivation of the sac fungi as suggested in the above theories has been fully discussed in the preceding pages.

II. *Descent from the Phycomycetes*.—De Bary ('81, '84, '87), as already stated in the first part of this paper, believed the *Ascomycetes* were derived from the *Phycomycetes*, particularly through such forms as the *Peronosporales*. The criterion for the *relationship* is the close homology and morphological resemblance of the sexual organs, though he suggested that *Eremascus* might have been derived from the *Mucorales* through some such form as *Piptocephalus* where

the zygote is the outgrowth from the fusion point of two equal gametangia.

Brefeld ('89, '91) also derived the *Ascomycetes* from the *Phycomycetes* but interpreted the ascus as the phyletic homologue of the sporangium, the ascus representing a specialized structure derived from the generalized sporangium in one direction, while the conidia were regarded as reduced one-spored sporangia. But the nuclear fusion and reduction phenomena in the ascus are so fundamentally different from any known cytological processes in the sporangium, that its phyletic relation to the sporangium is doubtful.¹ The conjugation of the gametangia he interpreted as ordinary fusion of hyphae which occurs in numerous instances devoid of all sexual significance. *Protomyces*, *Ascoidea* and *Thelebolus*, with numerous spores in the ascus, were interpreted as representing an intermediate condition between the generalized sporangium of the *Mucorales* and the specialized ascus. In *Thelebolus* it has been found that the development of the ascus follows the type with crozier formation and that it is closely related to *Ascobolus* and *Rhyparobius* (see Ramlow, '06; Dangeard, '07). As for *Protomyces* and *Ascoidea* they probably represent forms with reduced sexuality while retaining the ancestral character of many divisions of nuclei to form numerous spores.

Zukal ('89), influenced by Brefeld, derived the hymenial *Ascomycetes* (like *Ascobolus*, *Pezizales*, etc.) through *Thelebolus* and *Monascus*; the stromatic *Ascomycetes* (whether *Pyrenomycetes* or *Discomycetes*) from the *Uredinales*; the *Gymnoascales* and others with asci arising directly from the mycelium, from another ancestral type.

Lotsy ('07, p. 469) sees no difficulty in deriving the polyenergid forms like *Pyronema* from the *Phycomycetes*. The forms with spermatia, which are usually monoenergid, it would seem rational, he thinks, to derive from the red algae, and this raises the question as to whether the *Ascomycetes* are of polyphyletic (or biphyletic) origin. The great uniformity of the

¹ The nuclear phenomena in the "germ" sporangium (from the zygote) are not known.

ascus in the entire group is a great obstacle in the way of accepting a polyphyletic origin for the group. All things considered he is inclined to accept de Bary's view of their phycomycetous origin.

The origin of the *Ascomycetes* from the *Phycomycetes* is recognized by Dangeard ('07) through such forms in which there is still a union of gametangia. *Dipodascus* and *Eremascus* represent such forms in his scheme. The generalized ascus resulting from the union of the gametangia of *Dipodascus* he terms a "sporogone." From *Eremascus*, by reduction, forms like *Endomyces* arose, while the *Ascomycetes* with ascogenous hyphae were derived from such forms as *Dipodascus* by delayed nuclear fusion and the proliferation of the gametangium into what he terms "gametophores" (= ascogenous hyphae). The gametes then are formed in the nuclear pair which fuses in the ascus. This terminology arises from his persistent belief that the ascus is the egg. Shorn of the change in terminology and his, perhaps, unfortunate insistence on homologizing the ascus with the egg, his interpretation of the relation which such a form as *Dipodascus* bears to the *Ascomycetes*, has much merit.

Nienburg ('14) suggests the origin of the *Ascomycetes* from the *Phycomycetes* through some such form as *Monoblepharis*. He would find the evidence for this in the homology of the archicarp of *Polystigma rubrum* with such forms of *Monoblepharis* in which the stalk cell of the oogonium is an antheridium, and where the oogonium is terminated by one or more sterile cells. The archicarp of *Polystigma* he interprets as having two fertile cells at the base and prolonged into a long sterile septate portion (so-called trichogyne) which forks, sending a branch to either surface of the leaf. The basal multinucleate cell is the antheridium. After pore formation one nucleus migrates into the unicellular egg. Interesting as this suggestion is, forms of *Pythium* (see de Bary, '81, '84; Atkinson, '95) with intercalary oogonia and stalk antheridia present a closer analogy to the archicarp of *Polystigma* as described by Nienburg, but it is extremely doubtful if the point of contact is to be sought through such structures.

Brief comparative summary of the above views on the phylogeny of the Ascomycetes.—The adherents to the doctrine of the red algal origin of the *Ascomycetes* interpret the point of contact in three different ways: *first*, sac fungi with highly developed “trichogyne” (sterilized archicarp) of the *Collema* type with red algae like certain of the existing forms, *Nemalion*, or some of the higher forms in the vicinity of *Harveyella*, etc.; *second*, sac fungi with highly developed “trichogyne” (= sterilized archicarp) of the *Polystigma* type with hypothetical trichogyne algae representing the common stock for the origin of both groups; *third*, sac fungi with simple generalized copulating gametes of the *Gymnoascus* type with hypothetical algae having a simple procarp representing the stock from which both groups originated.

According to the two first interpretations the sac fungi have been derived through highly developed and specialized forms from either quite highly developed and specialized red algae, or both groups from a common trichogyne algal stock, and then by degeneration have slid backward from complex and specialized structures to simple, generalized and primitive ones. The third view which recognizes a simple procarp, without regard to a trichogyne, as the important character of the hypothetical stock, is far more comprehensible.

But if we must go back to some hypothetical ancestor, which cannot be represented by any known red alga, for the source of the sac fungi it is far more reasonable to search for one in another fungus line, where, in the light of present-day knowledge, there are known forms with sexual organs very much like the sexual organs of simple, known forms of the *Ascomycetes*. But we are not yet in a position to name any known phycomycete¹ as a probable ancestor of the *Ascomycetes*, though it appears very likely that the ancestral stock possessed phycomycetous characters.

¹ Lotsy ('07) suggests *Cystopus*; Miss Dale ('03) in her study of *Gymnoascus* suggests *Basidiobolus*; Nienburg ('14), *Monoblepharis*; while Dangeard ('07) suggests *Myzocyttium vermicolum* as the prototype of the higher fungi.

PROVISIONAL ARRANGEMENT OF MAIN LINES OF DEVELOPMENT IN
ASCOMYCETES

For those who are interested in the suggestions as to the phylogeny and relationships of the *Ascomycetes* presented in this paper, a diagrammatic arrangement of the principal series or lines which will illustrate the relationships tentatively held by the writer may be acceptable. It is with considerable hesitation that this arrangement is presented. The writer trusts that it will be accepted as provisional and in the nature of a working hypothesis which he hopes will further stimulate investigation, suggestions and criticisms on the ideas embodied in this paper, all of which, for or against, will be gladly welcomed.

Dipodascus, a primitive form, cells of mycelium polyenergid, gametogenous branches large, unequal, polyenergid. Ascus is elongated, broadened zygosporangium, zygote germinating immediately forming a broad germ tube in which spores are formed. Since the process does not go on to the formation of a sporangium, a different mode of internal free cell-formation then arose in connection with the precocious formation of spores in the zygote and retention of epiplasm which assists in discharge of spores. *Dipodascus* retains tendency of gametogenous branches to copulate early before they become strongly differentiated as gametangia, just as in *Mucorales*.

I. PROTOASCOMYCETES are derived by descent and degeneration from some such primitive ascomycete form as *Dipodascus*. The ascus when of sexual origin is the zygote, except in *Nadsonia*.

Endomyces Magnusii is the nearest known form to the generalized condition seen in *Dipodascus*. Cells of mycelium usually polyenergid, those of stout mycelium are polyenergid. Formation of ascus in *Endomyces Magnusii* repeats formation of zygosporangium in *Zygorhynchus*. Gamete branches in both are multinucleate, but when cell wall is laid down delimiting the gametangia all but one nucleus in each gametangium of *E. Magnusii* are excluded. After contact of the two sexual branches the male gametangium is formed by enlargement of its tip, into which protoplasm and the one nucleus migrates,

exactly as male gamete of *Zygorhynchus* is formed, except the latter is multinucleate. By disappearance of the separating wall, ascus is formed of the two gametes.

Endomyces series, then, derived from *Dipodascus*-like ancestors, with *Endomyces Magnusii* the lowest and most generalized.

Developmental tendencies from here in four, five, or six different directions:

1. *Eremascus*, both gamogenic branches uninucleate, ascus more definite and specialized in shape. Loss of conidial formation. *Endomyces fibuliger* indicates step toward *Eremascus* (*E. fertilis*) in small size of gametes.
2. *Endomyces* diverging into the two series, one chiefly with sprout conidia, the other chiefly with oidia; the latter preserves the *E. Magnusii* character, the former takes on sprout conidia in addition to oidia (*E. fibuliger* and *E. capsularis* form both oidia and sprout conidia); oidia formation the more primitive and generalized condition in *Ascomycetes*.
3. *Saccharomyces*. Still more specialized and reduced than in *Endomyces fibuliger* and in this same line. *Schizosaccharomyces* may have come from same line with dropping of sprout conidia, or may be descended from form near *Endomyces Magnusii*.
4. *Exoascaceae*. From *Endomyces*-like ancestors. Nuclear phenomena not well known. Diploid young ascus may have arisen in connection with cell wall formation, two nuclei being retained in ascogone instead of one as in *E. Magnusii*, where all but one are excluded at time of wall formation, i. e., ascus fundament may have retained the polyenergid character of the most primitive forms like *E. Magnusii*. Tendency to form hymenia may be controlled by host since asci in all, except *Taphrina laurencia*, come to surface to mature.
5. *Ascocorticium*, saprophytic on wood where food is not so rich, tendency to drop conidial formation (?), association of asci in hymenium, highest development of the *Endomyces* series, or of the *Protoascomycetes*. Series is terminated early, tendency in *Endomyces* line to specialization of zygote into one ascus with reduced number of spores, and line soon terminated.
6. *Ascoidea*, *Protomyces*, *Taphridium*, etc., probably represent forms derived by reduction and loss of distinct sexual organs but preserving primitive feature of many divisions of nucleus in the generalized ascus.

II. EUASCOMYCETES. Lowest forms with generalized archi-carp. Similar to *Monascus*, *Gymnoascus*, etc.

1. *Tendency* to late copulation of gamogenic branches, so that archicarp becomes large and many-nucleate, or tendency to elongate, or both.
2. As it elongates *tendency* to septation, first a single terminal cell ("trichogyne"), and later longer and multiseptate "trichogyne," or rather sterilization of terminal portion of archicarp. One of the early tendencies in connection with elongation of the archicarp may have been the origin of a receptive terminal portion under chemotactic or similar stimulation; such a condition suggested in *Cystopus*.
3. This made the passage of antheridial nuclei increasingly difficult, and resulted in early *tendency* to sterilization of antheridium or failure to function because of functionless condition of "trichogyne." Led in many cases to modified sexuality by differentiation of sex among nuclei in ascogonium, vegetative cells, or ascogenous threads.
4. *Progressive tendency* to multiplication of spores by postponement of nuclear fusion and spore formation: conjugate division of sex nuclei, and multiplication of the specialized structures (asci) in which spores are formed, so that spore formation and distribution is extended over greater period of time. This most advantageously attained by sprouting of zygote (ascogone), branching of threads, and terminal formation of specialized asci.

Diverging lines from *Gymnoascus* and *Monascus*-like ancestors or related prototypes in which asci are irregularly arranged but associated in groups with imperfect envelope.

1. A line with interwoven asci, *Plectascales* as a highly specialized lateral group, with *Gymnoascaceae* at base. *Aspergillaceae* a progressive line, with *Perisporiales* an offshoot, or *Perisporiales* direct from *Monascus*-like ancestors.
2. *Elaphomyetaceae*, asci interwoven in groups but separated by sterile walls.
3. *Pezizales*, asci remaining in groups not interwoven in mycelium, but spaced by sterile threads (paraphyses). *Pyronema* represents one of the generalized, lower forms. The *Helvellales*, etc., are probably derived from the *Pezizales*.
4. The *Microthyriales*¹ have usually been placed among the *Perisporiales* with which they have little in common. I believe they

¹Recent studies by several authors, particularly by von Höhnelt ('10) and by Theissen ('12, '13, '14) have greatly increased our knowledge of these interesting fungi, partly by the discovery of new forms but especially by uncovering many forms from the clouded situation in which they have been placed for lack of an adequate study of their structure.

represent reduced forms derived on the one hand from the *Phacidiales* and perhaps on the other from the *Sphaeriales* and possibly some from the *Perisporiales*. The formation of the characteristic shield has rendered superfluous the perithecial wall as a protective structure. The genus *Diplocarpon*, the structure and development of which was investigated by one of my former students (see Wolf, '12), I believe is an excellent illustration of a form on the way (by reduction of the perithecial wall in conjunction with the formation of the shield) from the *Phacidiales* to the condition presented by many members of the *Microthyriales*.

The above provisionally suggested relationships may be represented by the following five or six series, or lines of development, with the accompanying diagram (fig. 10):

1. Apocarp line from *Dipodascus*-like forms and by reduction.
2. Plectocarp line from *Dipodascus*-like forms, perhaps similar to *Monascus*.
3. Perispore line arising from *Monascus*-like prototype, before splitting of archicarp, or from *Aspergillaceae*.
4. Pyrenocarp line arising near *Monascus*-like prototype. *Laboulbeniales* side line near base, and some of the *Mycrothyriales* as reduced from *Sphaeriales*.
5. Discocarp line from *Dipodascus*-like forms near *Monascus*, but lower (it is not improbable that some of the members of the stock of primitive *Euscomycetes* showed considerable variation in the strength of the ascocarp envelope, also in its presence or absence in forms where it is more or less rudimentary¹); and some of the *Microthyriales* as reduced forms from *Phacidiales*.

Or a 6th line also, *Laboulbeniales* from *Monascus*-like ancestor.

¹ This variation sometimes occurs in existing forms. Zukal ('89) describes an abnormal case in *Eurotium* (*Aspergillus*) *herbariorum* where the antheridial branch and envelope are wanting, the mass of asci being exposed. In this connection it is worthy of note that Fraser and Chambers ('07) regard *Aspergillus* "as representing a primitive ascomycetous type from which most others can be derived." This suggestion was based on the assumption that the red algae were the ancestors of the sac fungi. On the basis of the counter theory (phycomycetous origin) *Gymnoascus* and *Monascus*-like forms are more comprehensible as primitive *Euscomycetes*.

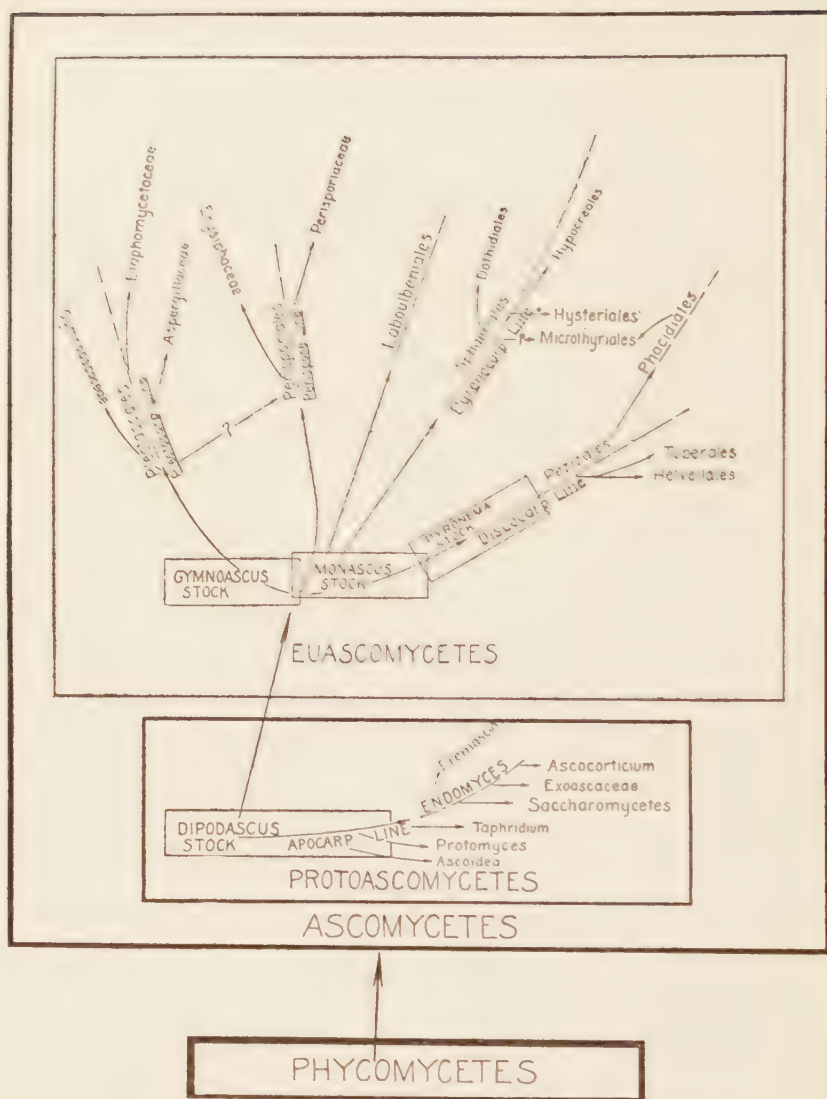


Fig. 10. Chart showing suggested phylogeny of the *Ascomycetes*.

LITERATURE CITED

- Atkinson, Geo. F. ('95). Damping off. Cornell Univ. Agr. Exp. Sta., Bull. 94: 231-272. pl. 1-6. 1895.
- Bachmann, Miss F. M. ('12). A new type of spermatogonium and fertilization in *Collema*. Ann. Bot. 26: 747-760. pl. 69. 1912.
- , ('13). The origin and development of the apothecium in *Collema pulposum* (Bernh.) Ach. Archiv f. Zellforsch. 10: 369-430. pl. 30-36. 1913.

- Barker, B. T. P. ('03). The morphology and development of the ascocarp in *Monascus*. *Ann. Bot.* 17: 167-236. *pl.* 12-13. 1903.
- , ('04). Further observations on the ascocarp of *Rhyarobius*. *British Assoc. Adv. Sci., Cambridge, Rept.* 1904: 825-826. 1905.
- de Bary, A. ('81). Untersuchungen über die Peronosporéen und Saprolegnieen und die Grundlagen eines natürlichen Systems der Pilze. In de Bary und Woronin, *Beitr. z. Morph. u. Physiol. d. Pilze* 4: 1-145. *pl.* 1-6. 1881.
- , ('84). Vergleichende Morphologie und Biologie der Pilze, usw. Leipzig, 1884.
- , ('87). Comparative Morphology and Biology of the Fungi, Mycetozoa, and Bacteria. 1887.
- Baur, E. ('98). Zur Frage nach der Sexualität der Collemaceen. *Ber. d. deut. bot. Ges.* 16: 363-367. *pl.* 23. 1898.
- , ('04). Untersuchungen über die Entwicklungsgeschichte der Flechten-
apothecien. *Bot. Zeit.* 62: 21-44. *pl.* 1-2. *f.* 1. 1904.
- Bessey, C. E. ('14). Revisions of some plant phyla. *Univ. Neb. Stud.* 14: 37-109. 1914.
- Bessey, E. A. ('13). Some suggestions as to the phylogeny of the Ascomycetes. *Myc. Centralbl.* 3: 149-153. 1913.
- Blackman, V. H. ('98). On the cytological features of fertilization and related phenomena in *Pinus sylvestris* L. *Roy. Soc. London, Bot., Phil. Trans.* 190: 395-427. *pl.* 13-14. 1898.
- , ('04). On the fertilization, alternation of generations and general cytology of the Uredineae. *New Phytol.* 3: 23-28. 1904.
- , ('04). On the fertilization, alternation of generations and general cytology of the Uredineae. *Ann. Bot.* 18: 323-373. *pl.* 21-24. 1904.
- , and Fraser, H. C. I. ('05). Fertilization in *Sphaerotheca*. *Ann. Bot.* 19: 567-569. 1905.
- , ———, ('06). On the sexuality and development of the ascocarp of *Humaria granulata* Quel. *Roy. Soc. London, Bot., Proc.* 77: 354-368. *pl.* 13-15. 1906.
- , ———, ('06). Further studies on the sexuality of the Uredineae. *Ibid.* 20: 35-48. *pl.* 3-4. 1906.
- , and Welsford, E. J. ('12). The development of the perithecium of *Polystigma rubrum* DC. *Ann. Bot.* 26: 761-767. *pl.* 70-71. 1912.
- Boveri, Th. ('88). Zellen Studien II. Die Befruchtung und Zellteilung des Eies von *Ascaris megalocephala*. Jena, 1888.
- Brefeld, O. ('88). Basidiomyceten II. Protobasidiomyceten. Untersuchungen aus dem Gesamtgebiete der Mykologie 7: I-X and 1-178. *pl.* 1-11. 1888.
- , ('89). Basidiomyceten III. Autobasidiomyceten und die Begründung des natürlichen Systemes der Pilze. *Ibid.* 8: 1-274. *pl.* 1-11. 1889.
- , ('91). Die Hemiasci und die Ascomyceten. *Ibid.* 9: 1-156. *pl.* 1-3B. 1891.
- , ('91). Ascomyceten II. *Ibid.* 10: 157-378. *pl.* 4-13. 1891.
- Brooks, F. T. ('10). The development of *Gnomonia erythrostoma* Pers. *Ann. Bot.* 24: 585-605. *pl.* 48-49. 1910.

- Brown, H. B. ('13). Studies in the development of *Xylaria*. *Ann. Myc.* 11: 1-13. *pl.* 1-2. 1913.
- Brown, W. H. ('09). Nuclear phenomena in *Pyronema confluens*. Preliminary note. *Johns Hopkins Univ. Circ. N. S.* 28^a: 42-45 (1-6). *f.* 1-3. 1909.
- , ('10). The development of the ascocarp of *Leotia*. *Bot. Gaz.* 50: 443-459. *f.* 1-47. 1910.
- , ('11). The development of the ascocarp of *Lachnea scutellata*. *Ibid.* 52: 273-305. *pl.* 9. *f.* 1-51. 1911.
- Carruthers, C. ('11). Contributions to the cytology of *Helvella crispa*. *Ann. Bot.* 25¹: 243-252. *pl.* 18-19. 1911.
- Chmielewski, W. F. ('90). Matériaux pour servir à la morphologie et physiologie des procès sexuels chez les plantes inférieures. 1890.
- Chodat, R. ('10). Etudes, sur les Conjugées I. Sur la copulation d'un *Spirogyra*. *Soc. Bot. Genève, Bull. II.* 2: 158-167. *f. a-g.* 1910.
- Christman, A. H. ('05). Sexual reproduction in the rusts. *Bot. Gaz.* 39: 267-275. *pl.* 8. 1905.
- , ('07). The nature and development of the primary uredospore. *Wis. Acad. Sci., Trans.* 15: 517-526. *pl.* 29. 1907.
- Claussen, P. ('05). Zur Entwicklungsgeschichte der Ascomyceten. *Boudiera. Bot. Zeit.* 63: 1-28. *pl.* 1-3. *f.* 1-6. 1905.
- , ('07). Zur Kenntnis der Kernverhältnisse von *Pyronema confluens*. *Ber. d. deut. bot. Ges.* 25: 586-590. *f.* 1. 1907.
- , ('08). Ueber Eientwicklung und Befruchtung bei *Saprolegnia*. *Ibid.* 26: 144-161. *pl.* 6-7. 1908.
- , ('12). Zur Entwicklungsgeschichte der Ascomyceten. *Pyronema confluens*. *Zeitschr. f. Bot.* 4: 1-64. *pl.* 1-6. *f.* 1-10. 1912.
- Cutting, E. M. ('09). On the sexuality and development of the ascocarp in *Ascophanus carneus* Pers. *Ann. Bot.* 23: 399-417. *pl.* 28. 1909.
- Dale, Miss E. ('03). Observations on the Gymnoasceae. *Ann. Bot.* 17: 571-596. *pl.* 27-28. 1903.
- , ('09). On the morphology and cytology of *Aspergillus repens*. *Ann. Myc.* 7: 215-225. *pl.* 2-3. 1909.
- Dangeard, P. A. ('92). Recherches sur la reproduction sexuelle des champignons. *Le Botaniste* 3: 222-281. *pl.* 20-23. 1892.
- , ('94). La reproduction sexuelle des Ascomycetes. *Ibid.* 4: 21-58. *f.* 1-10. 1894.
- , ('97). La reproduction sexuelle des Ascomycetes. *Ibid.* 5: 245-284. *f.* 1-17. 1897.
- , ('07). Recherches sur le développement du périthèce chez les Ascomycetes. *Ibid.* 10: 1-385. *pl.* 1-91. 1907.
- Darbshire, O. V. ('00). Über die Apothecienentwicklung der Flechte *Physcia pulverulenta* (Schreb.) Nyl. *Jahrb. f. wiss. Bot.* 34: 329-345. *pl.* 11. 1900.
- Davis, B. M. ('96). The fertilization of *Batrachospermum*. *Ann. Bot.* 10: 49-76. *pl.* 6-7. 1896.
- , ('03). Oögenesis in *Saprolegnia*. *Bot. Gaz.* 35: 233-249, 320-349. *pl.* 9-10. 1903.

- Dodge, B. O. ('12). Artificial cultures of *Ascobolus* and *Aleuria*. *Mycologia* 4: 218-222. *pl.* 72-73. 1912.
- , ('12a). Methods of culture and the morphology of the archicarp in certain species of the *Ascobolaceae*. *Bull. Torr. Bot. Club* 39: 139-197. *pl.* 10-15. *f.* 1-2. 1912.
- , ('14). The morphological relationships of the *Florideae* and the *Ascomycetes*. *Ibid.* 41: 157-202. *f.* 1-13. 1914.
- Eidam, E. ('80). Beitrag zur Kenntniss der Gymnoasceen. *Beitr. z. Biol. d. Pfl.* 3: 267-305. *pl.* 12-15. 1880.
- , ('83). Zur Kenntniss der Entwicklung bei den *Ascomyceten*. *Ibid.* 3: 376-433. *pl.* 19-23. 1883.
- , ('86). *Basidiobolus*, eine neue Gattung der *Entomophthoraceen*. *Ibid.* 4: 181-251. *pl.* 9-12. 1886.
- Fairchild, D. G. ('97). Ueber Kerntheilung und Befruchtung bei *Basidiobolus ranarum* Eidam. *Jahrb. f. wiss. Bot.* 30: 285-296. *pl.* 13-14. 1897.
- Faull, J. H. ('05). Development of ascus and spore formation in *Ascomycetes*. *Boston Soc. Nat. Hist., Proc.* 32: 77-113. *pl.* 7-11. 1905.
- , ('11). The cytology of the *Laboulbeniales*. *Ann. Bot.* 25: 649-654. 1911.
- , ('12). The cytology of *Laboulbenia chaetophora* and *L. Gyrinidarum*. *Ann. Bot.* 26: 325-353. *pl.* 37-40. 1912.
- Ferguson, Margaret C. ('01). The development of the egg and fertilization in *Pinus Strobilus*. *Ann. Bot.* 15: 435-479. *pl.* 22-25. 1901.
- , ('04). Contributions to the knowledge of the life history of *Pinus* with special reference to sporogenesis, the development of the gametophytes and fertilization. *Washington Acad. Sci., Proc.* 6: 1-202. *pl.* 1-24. 1904.
- Fisch, C. ('82). Beiträge zur Entwicklungsgeschichte einiger *Ascomyceten*. *Bot. Zeit.* 40: 851-905. *pl.* 10-11. 1882.
- Frank, A. B. ('83). Ueber einige neue und weniger bekannte Pflanzenkrankheiten. II. *Polystigma rubrum*. *Ber. d. deut. bot. Ges.* 1: 58-62. 1883.
- , ('86). Ueber *Gnomonia erythrostoma*, die Ursache einer jetzt herrschenden Blattkrankheit der Süßkirschen im Altenlande, nebst Bemerkungen über Infection bei blattbewohnenden *Ascomyceten* der Bäume überhaupt. (Vorläufige Mittheilung.) *Ibid.* 4: 200-205. 1886.
- Fraser, Miss H. C. I. ('07). On the sexuality and development of the ascocarp in *Lachnea stercorea*. *Ann. Bot.* 21: 349-360. 1907.
- , ('08). Contributions to the cytology of *Humaria rutilans* Fries. *Ann. Bot.* 22: 35-55. *pl.* 4-5. 1908.
- , ('13). The development of the ascocarp in *Lachnea cretea*. *Ibid.* 27: 553-563. *pl.* 42-43. 1913.
- , and Brooks, W. E. St. John ('09). Further studies on the cytology of the ascus. *Ibid.* 23: 537-549. *pl.* 34-40. *f.* 1. 1909.
- , and Chambers, H. S. ('07). The morphology of *Aspergillus herbariorum*. *Ann. Myc.* 5: 419-431. *pl.* 11-12. 1907.
- , and Welsford, E. J. ('08). Further contributions to the cytology of the *Ascomycetes*. *Ann. Bot.* 22: 465-477. *pl.* 26-27. 1908.

- Gates, R. R. ('09). The stature and chromosomes of *Oenothera gigas* De Vries. *Archiv. f. Zellforsch.* 3: 525-552. 1909.
- , ('13). Tetraploid mutants and chromosome mechanisms. *Biol. Centralbl.* 33: 92-150. *f.* 1-7. 1913.
- Guilliermond, A. ('08). La question de la sexualité chez les Ascomycetes. *Rev. Gen. Bot.* 20: 32-39, 85-89, 111-120, 178-182, 298-305, 333-334, 364-377. *f.* 1-86. 1908.
- , ('09). Recherches cytologiques et taxonomiques sur les Endomycetées. *Ibid.* 21: 354-391, 401-419. *pl.* 13-19. 1909.
- , ('12). Les levures. 1-565. *f.* 1-163. Paris, 1912.
- Harper, R. A. ('95). Beitrag zur Kenntniss der Kerntheilung und Sporenbildung im Ascus. *Ber. d. deut. bot. Ges.* 13: (67)-(68). *pl.* 27. 1895.
- , ('95a). Die Entwicklung des Peritheciums bei *Sphaerotheca Castagnei*. *Ibid.* 13: 475-481. *pl.* 89. 1895.
- , ('96). Ueber das Verhalten der Kerne bei der Fruchtentwicklung einiger Ascomyceten. *Jahrb. f. wiss. Bot.* 29: 655-685. *pl.* 11-12. 1896.
- , ('99). Cell-division in sporangia and asci. *Ann. Bot.* 13: 467-525. *pl.* 24-26. 1899.
- , ('00). Sexual reproduction in *Pyronema confluens* and the morphology of the ascocarp. *Ann. Bot.* 14: 321-400. *pl.* 19-21. 1900.
- , ('02). Binucleate cells in certain Hymenomycetes. *Bot. Gaz.* 33: 1-35. *pl.* 1. 1902.
- , ('05). Sexual reproduction and the organization of the nucleus in certain mildews. *Carnegie Inst. Washington, Publ.* 37: 1-104. *pl.* 1-7. 1905.
- Hartog, M. M. ('95). On the cytology of the vegetative and reproductive organs of the Saprolegnieae. *Roy. Irish Acad., Trans.* 30: 649-708. *pl.* 28-29. 1895.
- Hoffmann, A. W. H. ('12). Zur Entwicklungsgeschichte von *Endophyllum semipervivi*. *Centralbl. f. Bakt. II.* 32: 137-158. *pl.* 1-2. *f.* 1-14. 1912.
- von Höhnelt, F. ('10). Fragmente zur Mykologie. X. Mitteilung. *K. Akad. Wiss. Wien., Math.-naturw. Kl., Sitzungsber.* 119: 393-473 (1-81). *f.* 1. 1910.
- Janczewski, E. ('71). Morphologische Untersuchungen über *Ascobolus furfuraceus*. *Bot. Zeit.* 29: 257-262, 271-278. *pl.* 4. 1871.
- Juel, H. O. ('02). *Taphridium Lagerh. & Juel*. Eine neue Gattung der Protomycetaceen. *Bihang K. Sv. Vet.-Akad. Handl.* 27¹⁶: Afd. III. 1-29. *pl.* 1. 1902.
- , ('02). Über Zellinhalt, Befruchtung und Sporenbildung bei *Dipodascus*. *Flora* 91: 47-55. *pl.* 7-8. 1902.
- Karsten, G. ('08). Die Entwicklung der Zygoten von *Spirogyra jugalis* Ktzig. *Flora* 99: 1-11. *pl.* 1. 1908.
- Kihlman, O. ('83). Zur Entwicklungsgeschichte der Ascomyceten. *Soc. Sci. Fennicae, Acta* 13: 1-43. *pl.* 1-2. 1883.
- Kniep, H. ('13). Beiträge zur Kenntnis der Hymenomyceten, I, II. *Zeitschr. f. Bot.* 5: 593-637. *pl.* 2-5. *f.* 1. 1913.
- Kurssanow, L. ('11). Ueber Befruchtung, Reifung und Keimung bei *Zygnema*. *Flora* 104: 65-84. *pl.* 1-4. 1911.
- Lagerheim, G. de ('92). *Dipodascus albidus*, eine neue, geschlechtliche Hemiascee. *Jahrb. f. wiss. Bot.* 24: 549-565. *pl.* 24-26. 1892.

- Lindau, G. ('88). Ueber die Anlage und Entwicklung einiger Flechtenapothecien. *Flora* 71: 451-489. *pl.* 10. 1888.
- , ('99). Beiträge zur Kenntniss der Gattung Gyrophora. *Festschrift für Schwendener*. Berlin, 1899.
- Lotsy, J. P. ('07). Vorträge über botanische Stammesgeschichte 1: I-IV and 1-828. *f.* 1-430. 1907.
- Maire, R. ('99). Sur les phénomènes cytologiques précédant et accompagnant la formation de la téléospore chez le Puccinia Liliacearum Duby. *Compt. rend. acad. Paris* 129: 839-841. 1899.
- , ('01). L'évolution nucléaire chez les Urédinées et la sexualité. *Bull. Soc. Myc.* 17: 88-96. 1901.
- , ('02). Recherches cytologiques & taxonomiques sur les Basidiomycètes. *Ibid.* 18: 1-209. *pl.* 1-8. 1902.
- , ('03). Recherches cytologiques sur le Galactinia succosa. *Compt. rend. acad. Paris* 137: 769-771. 1903.
- , ('05). Recherches cytologiques sur quelques Ascomycetes. *Ann. Myc.* 3: 123-154. *pl.* 3-5. 1905.
- Marchal, É. et Ém. ('09). Aposporie et sexualité chez les Mousses. II. *Bull. acad. Belg. (classes des Sciences)* 1909: 1249-1288. 1909.
- , ('11). *Ibid.* III. *Ibid.* 1911: 750-778. *f.* 1-19. 1911.
- McCubbin, W. A. ('10). Development of the Helvellineae. I. *Helvella elastica*. *Bot. Gaz.* 49: 195-206. *pl.* 14-16. 1910.
- Mücke, M. ('08). Zur Kenntnis der Eientwicklung und Befruchtung von Achlya polyandra de Bary. *Ber. d. deut. bot. Ges.* 26^a: 367-378. *pl.* 6. 1908.
- Murrill, W. A. ('00). The development of the archegonium and fertilization in the hemlock spruce (*Tsuga canadensis* Carr.). *Ann. Bot.* 14: 583-607. *pl.* 21-22. 1900.
- Nichols, M. A. ('96). The morphology and development of certain pyrenomycetous fungi. *Bot. Gaz.* 22: 301-328. *pl.* 14-16. 1896.
- Nichols, S. P. ('04). The nature and origin of the binucleated cells in some Basidiomycetes. *Wis. Acad. Sci., Trans.* 15: 30-70. *pl.* 4-6. 1904.
- Nienburg, W. ('07). Beiträge zur Entwicklungsgeschichte einiger Flechtenapothecien. *Flora* 98: 1-40. *pl.* 1-7. 1907.
- , ('14). Zur Entwicklungsgeschichte von Polystigma rubrum DC. *Zeitschr. f. Bot.* 6: 369-400. *f.* 1-17. 1914.
- Olive, E. W. ('05). The morphology of Monascus pupureus. *Bot. Gaz.* 39: 59-60. 1905.
- , ('07). Cell and nuclear division in Basidiobolus. *Ann. Myc.* 5: 404-418. *pl.* 10. 1907.
- , ('08). Sexual cell fusions and vegetative nuclear divisions in the rusts. *Ann. Bot.* 22: 331-360. *pl.* 22. 1908.
- Oltmanns, F. ('98). Zur Entwicklungsgeschichte der Florideen. *Bot. Zeit.* 56: 99-140. *pl.* 4-7. 1898.
- , ('04). Morphologie und Biologie der Algen 1: 1-733. *f.* 1-467. Jena, 1904.
- Osterhout, W. J. V. ('00). Befruchtung bei Batrachospermum. *Flora* 87: 109-115. *pl.* 5. 1900.

- Overton, J. B. ('06). The morphology of the ascocarp and spore-formation in the many-spored asci of *Thecotheus Pelletieri*. Bot. Gaz. 42: 450-492. *pl.* 29-30. 1906.
- Raciborski, M. ('96). Studya Mykologiezne (Mycologische Studien I. Karyokinese bei *Basidiobolus ranarum*, *Absidia robusta* nov. sp., *Penicillium Poiraultii* nov. sp., *Entyloma Nymphaeae* Cunningham). Akad. d. Wiss., Krakau, Anz. 1896: 377-386. 1 *pl.* 19 *f.* 1896.
- Ramlow, G. ('06). Zur Entwicklungsgeschichte von *Thelebolus stercoreus* Tode. Bot. Zeit. 64: 85-99. 1906.
- , ('14). Beiträge zur Entwicklungsgeschichte der Ascoboleen. Myc. Centralbl. 5: 177-198. *pl.* 1-2, *f.* 1-20. 1914.
- Ruhland, W. ('01). Zur Kenntniss der intracellularen Karyogamie bei den Basidiomyceten. Bot. Zeit. 59: 187-206. *pl.* 7. 1901.
- Sachs, J. ('68). Lehrbuch der Botanik. 1-632. *f.* 1-465. Leipzig, 1868.
- , ('74). *Ibid.* 1874.
- , ('96). Physiologische Notizen X. Phylogenetische Aphorismen und über innere Gestaltungsursachen oder Automorphen. Flora 82: 173-223. 1896.
- Sappin-Trouffy, M. ('96). Recherches histologiques sur la famille des Urédinées. Le Botaniste 5: 59-244. *f.* 1-70. 1896.
- Schikorra, W. ('09). Ueber die Entwicklungsgeschichte von *Monascus*. Zeitschr. f. Bot. 1: 379-410. *pl.* 2, *f.* 1-3. 1909.
- Schmidle, W. ('99). Einiges über die Befruchtung, Keimung und Haarinsertion von *Batrachospermum*. Bot. Zeit. 57: 125-135. *pl.* F. 1899.
- Schmitz, F. ('79). Ueber die Fruchtbildung der Squamarien. Niederrhein. Ges. f. Nat.- u. Heilkunde, Bonn, Sitzungsber. 36: 376-377. 1879.
- , ('80). Ueber die Zellkerne der Thallophyten. *Ibid.* 37: 122-132. 1880.
- , ('83). Untersuchungen über die Befruchtung der Florideen. K. Preuss. Akad. Wiss., Berlin, Sitzungsber. 1883: 215-258. *pl.* 5. 1883.
- , und Hauptfleisch, P. ('97). Rhodophyceae. In Engler & Prantl, Nat. Pflanzenfam. 1³: 298-544. *f.* 192-288. Leipzig, 1897.
- Stahl, E. ('77). Beiträge zur Entwicklungsgeschichte der Flechten. 1-55. *pl.* 1-4. Leipzig, 1877.
- Stevens, F. L. ('99). The compound oosphere of *Albugo bliti*. Bot. Gaz. 28: 149-176, 225-245. *pl.* 11-15. 1899.
- , ('01). Gametogenesis and fertilization in *Albugo*. Bot. Gaz. 32: 77-98, 157-169, 238-261. *pl.* 1-4, *f.* 1. 1901.
- Stomps, T. J. ('12). Die Entstehung von *Oenothera gigas* deVries. Ber. d. deut. bot. Ges. 30: 406-416. 1912.
- Stoppel, R. ('07). *Eremascus fertilis* nov. spec. Flora 97: 333-346. *pl.* 11-12, *f.* 1-6. 1907.
- Strasburger, E. ('00). Über Reduktionsteilung, Spindelbildung, Centrosomen und Cilienbildner im Pflanzenreich. Histolog. Beitr. 6: 125. 1900.
- , ('04). Über Reduktionsteilung. K. preuss. Akad. Wiss. Berlin, phys.-math. Kl., Sitzungsber. 18: 587-615. *f.* 1-9. 1904.

- , ('05). Typische und allotypische Kernteilung, Ergebnisse und Erörterungen. Jahrb. f. wiss. Bot. 42: 1-71. 1905.
- , ('09). Sexuelle und apogame Fortpflanzung bei Urticaceen. Jahrb. f. wiss. Bot. 47: 245-288. pl. 7-10. 1909.
- Thaxter, R. ('96). Contribution toward a monograph of the Laboulbeniaceae. Am. Acad., Mem. 12: 189-429. pl. 1-26. 1896.
- , ('08). Contribution toward a monograph of the Laboulbeniaceae. II. *Ibid.* 13: 219-469. pl. 28-71. 1908.
- Theissen, F. ('12). Die Gattung *Clypeolela* v. Höhn. Centralbl. f. Bakt. II. 34: 229-235. 1912.
- , ('12). Fragmenta brasiliica IV nebst Bemerkungen über einige andere *Asterina*-Arten. Ann. Myc. 10: 1-32. f. 1-5. 1912.
- , ('12). Fragmenta brasiliica V nebst Besprechungen einiger palaeotropischer *Microthyriaceen*. Ann. Myc. 10: 159-204. 1912.
- , ('13). *Lembosia*-Studien. Ann. Myc. 11: 425-467. pl. 20. 1913.
- , ('13). *Hemisphaeriales*. (Vorläufige Mitteilung.) Ann. Myc. 11: 468-469. 1913.
- , ('13). Über einige *Mikrothyriaceen*. Ann. Myc. 11: 493-511. pl. 21. f. 1-7. 1913.
- , ('13). Die Gattung *Asterina* in systematischer Darstellung. K.K. zool.-bot. Ges., Wien, Abhandl. III. 7: 1-130. pl. 1-8. 1913.
- , ('13). Zur Revision der Gattungen *Mycrothyrium* und *Seynesia*. Österr. bot. Zeitschr. 63: 121-131. 1913.
- , ('14). *Trichopeltaceae* n. fam. *Hemisphaerialium*. Centralbl. f. Bakt. II. 39: 625-640. pl. 1. f. 1-7. 1914.
- , ('14). Über *Polystomella*, *Microcycus*, u. a. Ann. Myc. 12: 63-75. pl. 6-7. 1914.
- Treub, M. ('05). L'apogamie de *l'Elatostema acuminatum* Brogn. Ann. Jard. Bot. Buitenzorg II. 5: 141-152. pl. 4-11. 1905.
- Tröndle, A. ('07). Ueber die Kopulation und Keimung von *Spirogyra*. Bot. Zeit. 65: 187-210. pl. 5. f. 1-13. 1907.
- Twiss, W. C. ('11). *Erythrophyllum delesserioides* J. Ag. Univ. Calif. Publ. Bot. 4: 159-176. pl. 21-24. 1911.
- van Tieghem, Ph. ('84). Culture et développement du *Pyronema confluens*. Soc. Bot. France, Bull. 31: 355-360. 1884.
- De Vries, H. ('03). Die Mutations-Theorie 1; I-XIV and 1-752. pl. 1-2. f. 1-159. 1901; 2; I-XII and 1-648. pl. 1-8. f. 1-181. 1903.
- , ('13). Gruppenweise Artbildung unter spezieller Berücksichtigung der Gattung *Oenothera* I-VII and 1-365. pl. 1-22. f. 1-121. 1913.
- Vuillemin, P. ('12). Les champignons. Essai de classification. 1-425. Paris, 1912.
- Welsford, E. J. ('07). Fertilization in *Ascobolus furfuraceus*. New Phytol. 6: 156-161. pl. 4. 1907.
- Werth, E., and Ludwigs, K. ('12). Zur Sporenbildung bei Rost- und Brandpilzen. Ber. d. deut. bot. Ges. 30: 522-528. pl. 15. 1912.

- Wolf, F. A. ('12). The perfect stage of *Actinonema Rosae*. Bot. Gaz. **54**: 218-234. *pl. 13*. 1912.
- Wolfe, J. J. ('04). Cytological studies on *Nemalion*. Ann. Bot. **18**: 607-630. *pl. 40-41. f. 51*. 1904.
- Woronin, M. ('66). Zur Entwicklungsgeschichte des *Ascobolus pulcherrimus* Cr. und einiger *Pezizen*. In deBary und Woronin, Beitr. z. Morph. u. Physiol. d. Pilze **2**: 1-11. *pl. 1-4*. 1866.
- , ('70). *Sphaeria Lemaneae*, *Sordaria coprophila*, *fimiseda*, *Arthrobotrys oligospora*. *Ibid.* **3**: 1-36. *pl. 1-6*. 1870.
- Woycicki, Z. ('04). Einige neue Beiträge zur Entwicklungsgeschichte von *Basidiobolus ranarum*. Flora **93**: 87-97. *pl. 4. f. 1*. 1904.
- Yamanouchi, S. ('06). The life history of *Polysiphonia*. Bot. Gaz. **42**: 401-449. *pl. 19-28*. 1906.
- Zukal, H. ('89). Entwicklungsgeschichtliche Untersuchungen aus dem Gebiete der Ascomyceten. K. Akad. Wiss., Wien, Math.- naturw. Kl., Sitzungsber. **98**: 520-603. *pl. 1-4*. 1889.

A CONSPECTUS OF BACTERIAL DISEASES OF PLANTS

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All our knowledge of these diseases has come within a generation. It began thirty-six years ago with the announcement of the bacterial origin of pear blight by Professor T. J. Burrill of the University of Illinois, who is with us to-day. During the first half of that period progress was slow and doubt universal, especially in Europe.

It is now eighteen years since I ventured the statement,¹ that "there are in all probability as many bacterial diseases of plants as of animals." This statement was received with much skepticism, not to mention active opposition, but time has more than borne out my statement, and there is now no one left to dispute it. To-day I will venture another, and broader generalization, to wit: It appears likely that eventually a bacterial disease will be found in every family of plants, from lowest to highest. This prediction is based on the fact that although the field is still a very new one, with no workers in most parts of the world, such diseases have been reported from every continent, and are already known to occur in plants of one hundred and forty genera distributed through more than fifty families.

DISTRIBUTION

Following Engler's arrangement, I will list these families that you may see how wide is the distribution of bacterial diseases in plants and how utterly wrong were those who said that there were no such diseases, and also those who conceded a little but said that they were very rare and restricted to the soft underground parts of a few bulbous and tuberous plants, and generally preceded by fungi. In this list, I have included only the flowering plants, but some of the cryptogams are also

¹ *Am. Nat.* 30: p. 627. 1896.

subject to bacterial attack. The number following the family name indicates the number of bacterial diseases known within the limits of the family. The total of the figures, however, will not give the number of bacterial parasites, because some of the diseases overlap.

TABLE I

SHOWING THE FAMILIES OF FLOWERING PLANTS ARRANGED SERIALY FROM LOWEST TO HIGHEST. THOSE CONTAINING GENERA SUBJECT TO BACTERIAL DISEASES ARE UNDERScoreD, AND WHEN SEVERAL DISEASES HAVE BEEN RECOGNIZED THEIR NUMBER IS ALSO GIVEN

1. <u>Cycadaceae</u>	34. Juncaceae	68. Myzodendraceae
2. <u>Ginkgoaceae</u>	35. Stemonaceae	69. Santalaceae
3. Taxaceae	36. Melanthiaceae	70. Grubbiaceae
4. <u>Pinaceae 2</u>	37. <u>Liliaceae 3</u>	71. Opiliaceae
5. <u>Gnetaceae</u>	38. <u>Convallariaceae</u>	72. Olacaceae
6. Typhaceae	39. Smilacaceae	73. Balanophoraceae
7. Pandanaceae	36.)	74. Aristolochiaceae
8. Sparganiaceae	37.) <i>Liliaceae</i>	75. Rafflesiaceae
9. Potamogetonaceae	38.)	76. Hydnoraceae
10. Naiadaceae	39.)	77. Polygonaceae 2
11. Aponogetonaceae	40. Haemodoraceae	78. <u>Chenopodiaceae 4</u>
12. Scheuchzeriaceae	41. Amaryllidaceae	79. <u>Amaranthaceae</u>
12. <u>Juncaginaceae</u>	42. Velloziaceae	80. <u>Nyctaginaceae</u>
13. Alismaceae	43. Taccaceae	81. Batidaceae
14. Butomaceae	44. Dioscoreaceae	82. Theligonaceae
15. Vallisneriaceae	45. <u>Iridaceae</u>	82. <u>Cynocrambaceae</u>
15. <u>Hydrocharitaceae</u>	46. <u>Musaceae</u>	83. Phytolaccaceae
16. Triuridaceae	47. <u>Zingiberaceae</u>	84. Aizoaceae
17. Poaceae	48. Cannaceae	85. Portulacaceae
17. <u>Gramineae 7</u>	49. Marantaceae	86. Basellaceae
18. Cyperaceae	50. Burmanniaceae	87. Silenaceae
19. Phoenicaceae	51. <u>Orchidaceae</u>	87. <u>Caryophyllaceae 2</u>
19. <u>Palmae</u>	52. Casuarinaceae	88. Nymphaeaceae
20. Cyclanthaceae	53. Saururaceae	89. Ceratophyllaceae
21. <u>Araceae</u>	54. Piperaceae	90. Trochodendraceae
22. Lemnaceae	55. Chloranthaceae	91. <u>Ranunculaceae</u>
23. Flagellariaceae	56. <u>Salicaceae 2</u>	92. <u>Lardizabalaceae</u>
24. Baloskionaceae	57. <u>Myricaceae</u>	93. Berberidaceae
24. <u>Restionaceae</u>	58. Balanopsidaceae	94. Menispermaceae
25. Centrolepidaceae	59. Leitneriaceae	95. Magnoliaceae
26. Mayacaceae	60. <u>Juglandaceae 2</u>	96. Calycanthaceae
27. Xyridaceae	61. Betulaceae	97. Lactoridaceae
28. Eriocaulaceae	62. <u>Fagaceae</u>	98. Annonaceae
29. Rapateaceae	63. <u>Ulmaceae</u>	99. Myristicaceae
30. Bromeliaceae	64. Moraceae	100. Gomortegaceae
31. Commelinaceae	65. <u>Urticaceae 4</u>	101. Monimiaceae
32. Pontederiaceae	66. <u>Proteaceae</u>	102. Lauraceae
33. Phylodraceae	67. Loranthaceae	103. Hernandiaceae

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| 104. <u>Papaveraceae</u> | 140. <u>Tropaeolaceae</u> 3 | 184. <u>Malvaceae</u> 2 |
| 105. <u>Brassicaceae</u> | 141. <u>Linaceae</u> | 185. <u>Triplochitonaceae</u> |
| 105. <u>Cruciferae</u> 5 | 142. <u>Humiriaceae</u> | 186. <u>Bombacaceae</u> |
| 106. <u>Tovariaceae</u> | 143. <u>Erythroxylaceae</u> | 187. <u>Sterculiaceae</u> |
| 107. <u>Capparidaceae</u> | 144. <u>Zygophyllaceae</u> | 188. <u>Scytopetalaceae</u> |
| 108. <u>Resedaceae</u> | 145. <u>Cneoraceae</u> | 189. <u>Dilleniaceae</u> |
| 109. <u>Moringaceae</u> | 146. <u>Rutaceae</u> | 190. <u>Eucryphiaceae</u> |
| 110. <u>Sarraceniaceae</u> | 147. <u>Simaroubaceae</u> | 191. <u>Ochnaceae</u> |
| 111. <u>Nepenthaceae</u> | 148. <u>Balsameaceae</u> | 192. <u>Caryocaraceae</u> |
| 112. <u>Droseraceae</u> | 148. <u>Burseraceae</u> | 193. <u>Marcgraviaceae</u> |
| 113. <u>Podostemonaceae</u> | 149. <u>Meliaceae</u> | 194. <u>Quiniaceae</u> |
| 114. <u>Hydrostachyaceae</u> | 150. <u>Malpighiaceae</u> | 195. <u>Theaceae</u> |
| 115. <u>Crassulaceae</u> | 151. <u>Trigoniaceae</u> | 196. <u>Hypericaceae</u> |
| 116. <u>Penthoraceae</u> | 152. <u>Vochyaceae</u> | 197. <u>Clusiaceae</u> |
| 115. } <u>Crassulaceae</u> | 152. <u>Vochysiaceae</u> | 196. } <u>Guttiferae</u> |
| 116. } | 153. <u>Tremandraceae</u> | 197. } |
| 117. <u>Cephalotaceae</u> | 154. <u>Polygalaceae</u> | 198. <u>Dipterocarpaceae</u> |
| 118. <u>Saxifragaceae</u> | 155. <u>Dichapetalaceae</u> | 199. <u>Elatinaceae</u> |
| 119. <u>Hydrangeaceae</u> | 156. <u>Euphorbiaceae</u> | 200. <u>Frankeniaceae</u> |
| 120. <u>Escalloniaceae</u> | 157. <u>Callitrichaceae</u> | 201. <u>Tamaricaceae</u> |
| 121. <u>Grossulariaceae</u> | 158. <u>Buxaceae</u> | 202. <u>Fouquieriaceae</u> |
| 118. } | 159. <u>Coriariaceae</u> | 203. <u>Cistaceae</u> |
| 119. } | 160. <u>Empetraceae</u> | 204. <u>Bixaceae</u> |
| 120. } | 161. <u>Limnanthaceae</u> | 205. <u>Cochlospermaceae</u> |
| 121. } | 162. <u>Anacardiaceae</u> | 206. <u>Koeberliniaceae</u> |
| 122. <u>Pittosporaceae</u> | 163. <u>Cyrtillaceae</u> | 207. <u>Canellaceae</u> |
| 123. <u>Brunelliaceae</u> | 164. <u>Pentaphylacaceae</u> | 208. <u>Violaceae</u> |
| 124. <u>Cunoniaceae</u> | 165. <u>Corynocarpaceae</u> | 209. <u>Flacourtiaceae</u> |
| 125. <u>Myrothamnaceae</u> | 166. <u>Aquifoliaceae</u> | 210. <u>Stachyuraceae</u> |
| 126. <u>Bruniaceae</u> | 167. <u>Celastraceae</u> | 211. <u>Turneraceae</u> |
| 127. <u>Hamamelidaceae</u> | 168. <u>Hippocrateaceae</u> | 212. <u>Malesherbiaceae</u> |
| 128. <u>Platanaceae</u> | 169. <u>Stackhousiaceae</u> | 213. <u>Passifloraceae</u> |
| 129. <u>Crossosomataceae</u> | 170. <u>Staphyleaceae</u> | 214. <u>Achariaceae</u> |
| 130. <u>Rosaceae</u> | 171. <u>Icacinaceae</u> | 215. <u>Papayaceae</u> |
| 131. <u>Malaceae</u> | 172. <u>Aceraceae</u> | 215. <u>Caricaceae</u> |
| 132. <u>Amygdalaceae</u> | 173. <u>Aesculaceae</u> | 216. <u>Loasaceae</u> |
| 130. } | 173. <u>Hippocastanaceae</u> | 217. <u>Datisceae</u> |
| 131. } | 174. <u>Sapindaceae</u> | 218. <u>Begoniaceae</u> |
| 132. } | 175. <u>Sabiaceae</u> | 219. <u>Ancistrocladaceae</u> |
| 133. <u>Connaraceae</u> | 176. <u>Bersamaceae</u> | 220. <u>Cactaceae</u> |
| 134. <u>Mimosaceae</u> | 176. <u>Melanthaceae</u> | 221. <u>Geissolomaceae</u> |
| 135. <u>Caesalpinjiaceae</u> | 177. <u>Impatiensaceae</u> | 222. <u>Penaeaceae</u> |
| 136. <u>Krameriaceae</u> | 177. <u>Balsaminaceae</u> | 223. <u>Oliniaceae</u> |
| 137. <u>Fabaceae</u> | 178. <u>Rhamnaceae</u> | 224. <u>Thymelaeaceae</u> |
| 134. } | 179. <u>Vitaceae</u> 3 | 225. <u>Elaeagnaceae</u> |
| 135. } | 180. <u>Elaeocarpaceae</u> | 226. <u>Lythraceae</u> |
| 136. } | 181. <u>Schizolaenaceae</u> | 227. <u>Blattiaceae</u> |
| 137. } | 181. <u>Chlaenaceae</u> | 227. <u>Sonneratiaceae</u> |
| 138. <u>Geraniaceae</u> 2 | 182. <u>Gonystylaceae</u> | 228. <u>Crypteroniaceae</u> |
| 139. <u>Oxalidaceae</u> | 183. <u>Tiliaceae</u> | 229. <u>Punicaceae</u> |

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| 230. <u>Lecythidaceae</u> | 252. <u>Primulaceae</u> | 275. <u>Bignoniaceae</u> |
| 231. <u>Rhizophoraceae</u> | 253. <u>Plumbaginaceae</u> | 276. <u>Pedaliaceae</u> |
| 232. <u>Combretaceae</u> | 254. <u>Sapotaceae</u> | 277. <u>Martyniaceae</u> |
| 233. <u>Myrtaceae</u> | 255. <u>Diospyraceae</u> | 278. <u>Orobanchaceae</u> |
| 234. <u>Melastomataceae</u> | 255. <u>Ebenaceae</u> | 279. <u>Gesneriaceae</u> |
| 235. <u>Onagraceae</u> | 256. <u>Styracaceae</u> | 280. <u>Columelliaceae</u> |
| 236. <u>Trapaceae</u> | 257. <u>Symplocaceae</u> | 281. <u>Pinguiculaceae</u> |
| 236. <u>Hydrocaryaceae</u> | 258. <u>Oleaceae 2</u> | 281. <u>Lentibulariaceae</u> |
| 237. <u>Haloragidaceae</u> | 259. <u>Salvadoraceae</u> | 282. <u>Globulariaceae</u> |
| 237. <u>Halorrhagidaceae</u> | 260. <u>Loganiaceae</u> | 283. <u>Acanthaceae</u> |
| 238. <u>Cynomoriaceae</u> | 261. <u>Gentianaceae</u> | 284. <u>Myoporaceae</u> |
| 239. <u>Araliaceae 2</u> | 262. <u>Menyanthaceae</u> | 285. <u>Phrymaceae</u> |
| 240. <u>Apiaceae</u> | 261. } <u>Gentianaceae</u> | 286. <u>Plantaginaceae</u> |
| 240. <u>Umbelliferae 3</u> | 262. } | 287. <u>Rubiaceae</u> |
| 241. <u>Cornaceae</u> | 263. <u>Apocynaceae</u> | 288. <u>Caprifoliaceae</u> |
| 242. <u>Clethraceae</u> | 264. <u>Asclepiadaceae</u> | 289. <u>Adoxaceae</u> |
| 243. <u>Pyrolaceae</u> | 265. <u>Convolvulaceae</u> | 290. <u>Valerianaceae</u> |
| 244. <u>Monotropaceae</u> | 266. <u>Cuscutaceae</u> | 291. <u>Dipsacaceae</u> |
| 243. } <u>Pyrolaceae</u> | 265. } <u>Convolvulaceae</u> | 292. <u>Cucurbitaceae 3</u> |
| 244. } | 266. } | 293. <u>Campanulaceae</u> |
| 245. <u>Lennoaceae</u> | 267. <u>Polemoniaceae</u> | 294. <u>Goodeniaceae</u> |
| 246. <u>Ericaceae</u> | 268. <u>Hydrophyllaceae</u> | 295. <u>Candolleaceae</u> |
| 247. <u>Vacciniaceae</u> | 269. <u>Boraginaceae</u> | 296. <u>Calyceraceae</u> |
| 246. } <u>Ericaceae</u> | 270. <u>Verbenaceae</u> | 297. <u>Cicchoraceae</u> |
| 247. } | 271. <u>Menthaceae</u> | 298. <u>Ambrosiaceae</u> |
| 248. <u>Epacridaceae</u> | 271. <u>Labiatae</u> | 299. <u>Asteraceae</u> |
| 249. <u>Diapensiaceae</u> | 272. <u>Nolanaceae</u> | 297. } |
| 250. <u>Theophrastaceae</u> | 273. <u>Solanaceae 9</u> | 298. } <u>Compositae 3</u> |
| 251. <u>Myrsinaceae</u> | 274. <u>Scrophulariaceae</u> | 299. } |

The widest gap, it will be observed, is between *Cruciferae* and *Rosaceae*, but I believe this represents nothing more than lack of knowledge.

Also I should like to list the genera within the limits of which one or more species are now said to be subject to attack, because many of these genera contain plants of great economic importance. Where I have some personal knowledge of the subject I have italicized the genus name, and in what follows the reader will naturally expect me to draw illustrations principally from the diseases most familiar to me.

TABLE II

SHOWING GENERA OF FLOWERING PLANTS SUBJECT TO DISEASES OF BACTERIAL ORIGIN

Macrozamia	Bromus	Avena	Phleum
Pinus	Zea	Saccharum	Poa
Dactylis	Andropogon	Triticum	Cocos

<i>Oreodoxa</i>	<i>Beta</i>	<i>Prosopis</i> (?)	<i>Syringa</i>
<i>Richardia</i>	<i>Amaranthus</i>	<i>Erythrina</i>	<i>Olea</i>
<i>Amorphophallus</i>	<i>Dianthus</i>	<i>Geranium</i>	<i>Fraxinus</i>
<i>Hyacinthus</i>	<i>Delphinium</i>	<i>Pelargonium</i>	<i>Strychnos</i>
<i>Allium</i>	<i>Papaver</i>	<i>Tropaeolum</i>	<i>Nerium</i>
<i>Lilium</i>	<i>Brassica</i>	<i>Citrus</i>	<i>Tectona</i>
<i>Iris</i>	<i>Raphanus</i>	<i>Cedrela</i>	<i>Verbena</i>
<i>Ixia</i>	<i>Cheiranthus</i>	<i>Manihot</i>	<i>Capsicum</i>
<i>Gladiolus</i>	<i>Matthiola</i>	<i>Mangifera</i>	<i>Solanum</i>
<i>Musa</i>	<i>Amelanchier</i>	<i>Euonymus</i>	<i>Lycopersicum</i>
<i>Zingiber</i>	<i>Sorbus</i>	<i>Vitis</i>	<i>Nicotiana</i>
<i>Dendrobium</i>	<i>Eryobotrya</i>	<i>Gossypium</i>	<i>Physalis</i>
<i>Cattleya</i>	<i>Pyrus</i>	<i>Malva</i>	<i>Petunia</i>
<i>Oncidium</i>	<i>Cydonia</i>	<i>Sterculia</i>	<i>Datura</i>
<i>Odontoglossum</i>	<i>Prunus</i>	<i>Elodea</i>	<i>Calceolaria</i>
<i>Cypripedium</i>	<i>Rubus</i>	<i>Begonia</i>	<i>Sesamum</i>
<i>Phalaenopsis</i>	<i>Crataegus</i>	<i>Opuntia</i>	<i>Pavetta</i>
<i>Vanilla</i>	<i>Fragaria</i>	<i>Eucalyptus</i>	<i>Psychotria</i>
<i>Salix</i>	<i>Rosa</i>	<i>Oenothera</i>	<i>Benincasa</i>
<i>Populus</i>	<i>Heteromeles</i>	<i>Aralia</i>	<i>Cucumis</i>
<i>Juglans</i>	<i>Dolichos</i>	<i>Hedera</i>	<i>Cucurbita</i>
<i>Castanea</i>	<i>Lathyrus</i>	<i>Carota</i>	<i>Citrullus</i>
<i>Corylus</i>	<i>Indigofera</i>	<i>Pastinaca</i>	<i>Sicyos</i>
<i>Morus</i>	<i>Kraunhia</i> (?)	<i>Levisticum</i>	<i>Echinocystis</i>
<i>Pouzolzia</i>	<i>Lupinus</i>	<i>Apium</i>	<i>Ageratum</i>
<i>Cannabis</i>	<i>Mucuna</i>	<i>Arbutus</i>	<i>Chrysanthemum</i>
<i>Acalypha</i>	<i>Phaseolus</i>	<i>Vaccinium</i>	<i>Lactuca</i>
<i>Humulus</i>	<i>Vigna</i>	<i>Ardisia</i>	<i>Blumea</i>
<i>Ficus</i>	<i>Pisum</i>	<i>Crispandisia</i>	<i>Synedrella</i>
<i>Rheum</i>	<i>Trifolium</i>	<i>Amblyanthus</i>	<i>Tragopogon</i>
<i>Polygonum</i>	<i>Medicago</i>	<i>Amblyanthopsis</i>	<i>Bellis</i>
<i>Atriplex</i>	<i>Arachis</i>	<i>Diospyros</i>	<i>Aster</i>
<i>Spinacia</i>	<i>Acacia</i>	<i>Ligustrum</i>	

PERIOD OF GREATEST SUSCEPTIBILITY

In certain diseases the brief seedling stage of the plant is the one most subject to attack, e. g., Stewart's disease of maize due to *Bacterium Stewarti*, and brown rot of tomato and tobacco due to *Bacterium Solanacearum*, but many bacterial diseases of older plants are also rather strictly time-limited. In both groups it is a question of abundant immature tissue. To the latter class belong the numerous leaf-spots, fruit-spots, and blights, e. g., black spot on the plum and peach, due to *Bacterium Pruni*, and fire-blight of the pear, apple, quince, etc., due to *Bacillus amylovorus*. In such cases, so far at least as they occur in temperate climates, the disease appears in

the spring and the greater part of it occurs during a brief period in the early summer, in which growth of roots, leaves and shoots is proceeding rapidly and there are many young and succulent parts. The cause of the disease may and often does remain on the plant over winter in a latent or semi-latent condition (walnut blight, pear blight, plum canker), but the active period is limited to three months, more or less, of actively growing weather in which developing tissues, subject to infection, are abundant. With definitive growth and the hardening of the tissues in late summer and autumn, the disease is checked and disappears, or remains as a slow canker to appear again on other parts the following spring. It is a very instructive experiment to see, for example, inoculations of *Bacillus amylovorus* on ripening fruits and shoots of the pear wholly fail toward the end of July, which were eminently successful on the same trees at the beginning of June. The difference in this case is not due to lessened virulence on the part of the organism, but to changes in the host-plant, making it non-susceptible. Similar changes leading to non-susceptibility occur in the Japanese plum subject to *Bacterium Pruni*; the young fruits are very susceptible, the maturing fruits cannot be infected.

Other parasites on the contrary are able to attack, disintegrate and destroy matured tissues, e. g., the pith of cabbage stems, turnip roots, the ripened tubers of the potato, well developed roots of sugar beets, the bulbs of onions and hyacinths, full-grown melon and cucumber fruits.

In both of these types the action of the parasite is expended chiefly on the parenchyma, although in some cases (the plum disease, Appel's potato rot) there is more or less bacterial invasion of the local vessels. Vascular occupation is not a special characteristic.

In the typical vascular diseases the case is reversed. Here parenchyma is also destroyed, more or less, but the most conspicuous and destructive action is on the vascular bundles themselves, which are occupied for long distances, to the death, or great detriment, of the whole plant. In maize attacked by *Bacterium Stewarti*, it is not unusual, indeed one might rather

say it is customary, to find the vessels of the stem filled with the bacteria continuously for a distance of 3–6 feet from the point of infection, i. e., from the surface of the earth to the top of the full-grown plant. In cucurbits attacked by *Bacillus tracheiphilus* and in sugar-cane attacked by *Bacterium vascularum* the same thing occurs, and many of the vessels are filled solid with the bacterial slime to a distance of 8 or 10 feet from the place of infection. In such cases infection has taken place generally near the base of the plant, which continues to grow for some weeks or months.

Transitions, of course, occur. *Bacterium Stewarti*, for example, is confined much more strictly to the vascular bundles of the maize stem than is *Bacterium Solanacearum* to those of the tomato, potato, or tobacco stem, although it also is a vascular parasite; that is, following infection of the vessels we do not find in the maize stems that extensive breaking down of the pith and phloem into vast cavities which is so common, for example, in tobacco and tomato stems.

WHAT GOVERNS INFECTION

Within the plant we may suppose, from certain indications, that abundant juiciness is the chief factor governing the infection of immature tissues. To this may be added an abundant well-adapted food supply and, in some cases, probably the absence of inhibiting substances, which may appear later. As the parts approach maturity the water content becomes less. Along with this, acids, sugars, amids, proteids, etc., are consumed and converted into substances less well adapted to the needs of the meristem-parasites, if not wholly inimical. In young shoots of potato and tomato, or of pear and apple, as contrasted with old ones, or in the roots of carrots as compared with the leaves, or in rapidly-growing cabbages, as compared with slow-growing ones, we know that there is an excess of water, and this alone appears to be sufficient to explain the difference in behavior of their respective parasites in old versus young parts. When, however, we come to ripening fruits, such as the pear and the plum, it would seem that they are still juicy enough to favor the growth of almost any

bacterium, and we are forced to the hypothesis of chemical changes within the fruits to account for the failure of inoculations. As a rule (there are striking exceptions), parasitic micro-organisms are rather sensitive to changes in their environment, e. g., to drying, exhaustion of food supplies, multiplication of their own by-products, conversion of an easily assimilable substance into one less assimilable or actually harmful, appearance of esters, new acids, etc. But why speculate! Much additional experimenting must be undertaken before we shall have precise and full data. We are still largely in the observational stage.

The parasites of ripened tissues do not require so much water, are able to convert starch into sugar, or have a special liking for some other element of the plant tissue.

Externally, a number of factors favor infection. One of these is excessive shade, either of clouds or of foliage. Another is high temperature. When these two factors are accompanied by excessive rainfall, wet earth, and heavy dews, the conditions are ideal for the rapid dissemination and the destructive prevalence of a variety of bacterial diseases of cultivated plants. The bean spot due to *Bacterium Phaseoli*, the black spot of plum due to *Bacterium Pruni*, and the larkspur disease due to *Bacterium Delphinii*, are all favored by heavy dews and by shade. In hot, wet weather in July pear blight due to *Bacillus amylovorus* often bursts out like a conflagration and sweeps over whole orchards. In warm, moist autumns bacterial diseases of the potato may destroy almost or quite the entire crop over extensive districts.

HOW INFECTION OCCURS

As I have already described elsewhere how infection occurs,¹ I will only dwell for a moment on it here, offering a few examples.

The commonest way of infection is probably through wounds.

¹ Smith, E. F. Bacteria in relation to plant diseases. Carnegie Inst. Washington, Publ. 27²: pp. 51-64. 1911.

In Italy, the olive tubercle due to *Bacterium Savastanoi* has been observed to begin very often in wounds made by hail-stones. In South Africa, crown-gall is said to be disseminated in the same way. In this country and also in Sumatra, *Bacterium Solanacearum* enters the plant more often than otherwise through broken roots. A tomato or tobacco plant with unbroken roots will thrive in a soil deadly to one that has been root-pruned. I have myself observed this. We may suppose that substances attractive to the particular bacteria diffuse into the soil from the broken roots, following which they enter the plant. Resistant plants may be supposed to diffuse indifferent or repellant substances. All infections must be chemotactic.

More interesting perhaps are those diseases which begin in natural openings, i. e., in places where the protective covering of the plant gives place to special organs such as nectaries, water-pores, and stomata.

All the pome fruits subject to fire-blight are liable to blossom infection. The bacteria multiply first in the nectaries of the flower, passing down into the stem by way of the ovary and pedicel. Blossom blight of the pear is a very conspicuous and common form of the disease as everybody knows. Thousands of blighted blossom clusters may be seen in any large orchard subject to this disease.

In the black rot of the cabbage due to *Bacterium campestre*, the majority of the infections begin in the water-pores. These are grouped on the margins of the leaf at the tips of the serratures. From this point the bacteria burrow into the vascular system of the leaf and so pass downward into the stem and upward into other leaves.

In the black spot of the plum, almost or quite all of the infections are stomatal. A large proportion of them are also stomatal in the leaf-spot of cotton, and other leaf-spots.

TIME BETWEEN INFECTION AND APPEARANCE OF THE DISEASE

As in animal diseases, the period of latency may be very short or surprisingly long. Some time must be allowed the parasitic organism to multiply inside the plant before it does

damage serious enough to be recognized externally as a *disease*. This is the so-called "period of incubation," during which the parasite is growing and its enzymes and toxins are becoming active. The microscope shows it to be present in the tissues, but the latter have yielded only a little in the immediate vicinity of the bacterial focus. This time is short or long depending on whether the parasite or the host has the first advantage. If the host is growing rapidly it may either entirely outstrip the parasite, or be only so much the more subject to it. All depends on whether the parasite finds the initial conditions entirely suited to its needs, or by means of its secretions and excretions can quickly make them so, and consequently can from the start make a rapid growth, or must first slowly overcome obstacles of various sorts, such as inhibiting acids and resistant tissues. The plant may show signs of infection within as short a time as one or two days after inoculation (various soft rots), or it may be as long a time as one to two months before they appear (Cobb's disease of sugar-cane, Stewart's disease of sweet-corn). In the latter, infection generally occurs in the seedling stage and the maize plant may be three months old and six feet tall before it finally succumbs. Of course, as in case of bacterial animal diseases, the greater the volume of infectious material the shorter the time. I have seen many instances of that law. In general, the period of latency may be said to vary from one to three weeks (yellow disease of hyacinth, black rot of cabbage, black spot of plum, cucurbit wilt, pear blight, angular leaf-spot of cotton, sorghum leaf-stripe, etc.).

RECOVERY FROM DISEASE

Mention has already been made of the self-limited spot diseases and blights. As the actively growing season draws to a close such diseases cease their activity.

Also in some plants well developed signs of vascular disease may be suppressed (squash, maize, sugar-cane) or remain in abeyance for a longer or shorter period, according to the varying fortunes of the host and the capabilities of the parasite. The tomato plants inoculated with *Bacterium Sol-*

anacearum (Medan III) and photographed for Volume III of 'Bacteria in Relation to Plant Diseases' (plate 45 D), entirely outgrew the disease, as did also certain sugar-canes (series VI) inoculated with *Bacterium vascularum*.¹ Also, I have seen tomato plants recover only to develop a second and fatal attack of the vascular brown rot three months after the first attack, during which period they had made an extensive healthy-looking growth.²

Recovery from disease may depend on *loss of virulence* on the part of the parasite. This often occurs when bacteria are grown for some time on culture-media, and it occurs also in nature, but its cause is obscure.

AGENTS OF TRANSMISSION

These may be organic or inorganic. In many cases the plant itself harbors the parasite indefinitely, carrying it over from year to year on some portion of its growth.

Seeds, tubers, bulbs, grafts, or the whole plant may be responsible for the appearance of the disease the following year in the old localities, and through the agency of seedsmen, nurserymen, or whoever disseminates plants, for outbreaks in regions hitherto exempt.

There is good reason to believe that the black rot of cabbage and Stewart's disease of sweet corn have been disseminated broadcast in the United States in recent years by ignorant and unscrupulous seedsmen. Both diseases are transmitted to seedling plants from the seed. The yellow disease of hyacinths is carried in the bulb. Potato tubers from diseased fields may infect healthy fields. Apple grafts have transmitted crown-gall. Slightly infected trunks and limbs of trees (hold-over pear blight, walnut blight, canker of the plum) may infect shoots, leaves, blossoms, or fruits the following season. The soil around the infected plant may serve for years as a source of infection to other species (crown-gall), or to other individuals of the same kind (various leaf-spots). Occasionally, however, a parasite seems to die out of certain soils (*Bac-*

¹ Smith, E. F. Bacteria in relation to plant diseases. Carnegie Inst. Washington, Publ. 27^s: p. 33. 1914.

² *Ibid.* p. 179.

terium Solanacearum). The pear blight organism probably dies out of soils quickly as it does in a majority of the blighted branches. Pear blight by soil infection is not known.

Among extraneous agents, wind and water have been suspected. I have never seen any clear indications of wind-borne infection, not even when conditions seemed to invite it, but water often carries parasites and furnishes conditions favorable to infection. Horne has shown that the olive tubercle in California is transmitted in this way. Honing, in the tobacco fields of Sumatra, has traced infection several times to the watering of plants from infected wells, and has cultivated the parasite from the water. I have discovered experimentally that to obtain several sorts of bacterial leaf-spots (bean, cotton, peach, plum, carnation, larkspur, sorghum, geranium) the surface of the leaves must be kept moist to the same extent they would be in case of prolonged dews or frequent light showers. Such conditions are necessary to enable the bacteria to penetrate the stomata and begin to grow. In case of water-pores, however, the plant itself furnishes the water necessary for infection, if the nights are cool enough, i. e., if the air remains near enough to saturation to prevent for some hours the evaporation of the excreted water from the leaf-serratures. Every plant with functioning water-pores awaits its appropriate bacterial parasite. The genus *Impatiens* is a good example. I have looked on it for one in vain but I am sure it must occur.

Man and the domestic animals, especially through the agency of the dung-heap, infallible repository of all sorts of discarded refuse, undoubtedly help to spread certain bacterial diseases of plants (potato rots, black rot of cabbage, etc.).

Birds probably transmit some of these diseases on their feet or in other ways. In connection with the bud-rot of the coconut palm in the West Indies, I suspect the turkey-buzzard, but the evidence is not complete. Long since, Mr. Waite obtained (once in Florida, once in Maryland) the strongest kind of circumstantial evidence going to show that pear blight may be spread by birds.

Respecting insects, molluscs, and worms, the evidence is complete. They often serve to carry these diseases. I have summarized our knowledge in another place¹ and will here content myself with a brief statement calling renewed attention to the subject.

We had very good evidence of the transmission of one bacterial disease of plants by insects long before the animal pathologists awoke to the importance of the subject,² but it cannot be said that they have ever paid much attention to it, although it antedates by two years the work by Theobald Smith and Kilborne showing that Texas fever is transmitted by the cattle tick (*Ixodes bovis*). That discovery also belongs to the credit of the U. S. Department of Agriculture, and the two together may be said to have laid broad and deep the foundations of this most important branch of modern pathology. Waite isolated the pear blight organism, grew it in pure cultures, and proved its infectious nature by inoculations. With such proved cultures he sprayed clusters of pear flowers in places where the disease did not occur and obtained blossom-blight, and later saw this give rise to the blight of the supporting branch, found the organism multiplying in the nectar, and reisolated it from the blighting blossoms. On some trees he restricted the disease to the sprayed flowers by covering them with mosquito netting to keep away bees and other nectar-sipping insects. On other trees where the flowers were not covered he saw bees visit them, sip from the inoculated blossoms and afterwards visit blossoms on unsprayed parts of the tree which then blighted. Finally he captured bees that had visited such infected blossoms, excised their mouth parts, and from these, on agar-poured plates, obtained *Bacillus amylovorus*, with colonies of which he again produced the disease. These experiments were done in several widely separated localities with identical results. I saw them and they made a great impression on me.

¹ Smith, E. F. Bacteria in relation to plant diseases. Carnegie Inst. Washington, Publ. 27: p. 40. 1911.

² Waite, M. B. Results from recent investigations in pear blight. Bot. Gaz. 16: 259; Am. Assoc. Adv. Sci., Proc. 40: 315. 1891.

The writer has since proved several diseases to be transmitted by insects, notably the wilt of cucurbits, and here the transmission is not purely accidental, but there appears to be an adaptation, the striped beetle (*Diabrotica vittata*), chiefly responsible for the spread of the disease, being fonder of the diseased parts of the plant than of the healthy parts. This acquired taste, for it must be that, works great harm to melons, squashes, and cucumbers. Whether the organism winters over in the beetles, as I suspect, remains to be determined. Certainly the disease appears in bitten places on the leaves very soon after the spring advent of the beetles.

In 1897 I showed that molluscs sometimes transmit brown rot of the cabbage, and last year I saw indications in Southern France which lead me to think that snails are responsible for the spread of the oleander tubercle, i. e., I saw them eating both sound and tubercular leaves, and found young tubercles developing in the eroded margins of bitten leaves.

Parasitic nematodes break the root tissues and open the way for the entrance of *Bacterium Solanacearum* into tobacco and tomato, as was first observed by Hunger in Java and later by myself in the United States. One of the serious problems of plant pathology is how to control *Heterodera radicum*, not only because of its wide distribution on a great variety of cultivated plants and the direct injury it works, but also on account of the often very much greater injury it causes through the introduction into the roots of the plant of bacterial and fungous parasites. The man who shall discover an effective remedy will deserve a monument more enduring than brass. Our Southern States in particular are overrun with this parasite.

Much remains to be done before we shall know to what extent fungous parasites function as carriers of parasitic bacteria. H. Marshall Ward sought to explain the presence of bacteria in diseased plants by supposing that they must enter the plant through the lumen of fungous hyphae. In this he was wrong, certainly if it be stated as a general proposition, but it appears to be clear that in some cases the two types of parasites work together, the fungus invading first, and the

bacterium following hard after and often doing the major part of the damage. The reverse of this also occurs, the bacterium entering first and the fungus following.

Parasitic bacteria are soon followed by saprophytic bacteria which complete the destruction of the tissues, and, if the disease is somewhat advanced, cultures from the tissues may yield only the latter (potato rots). Also, as in animals, one parasitic disease may follow another and the second be more destructive than the first, e. g., fire-blight following crown-gall on the apple.

EXTRA-VEGETAL HABITAT OF THE PARASITES

Here is perhaps the place to say a few words about the non-parasitic life of the attacking organisms.

All are able to grow saprophytically, i. e., on culture media of one sort or another, and probably all live or may live for a time in the soil. Very few, however, have been cultivated from it. The vast mixture of organisms present in a good earth rather discourages search. In some of the unsuccessful attempts failure may have been due to not having undertaken isolations at exactly the right time, or in just the right place, or on just the proper medium, but more often probably to the swamping tendency of rapidly growing saprophytes. How long a parasite is able to maintain its virulent life in a soil must depend largely on the kind of competitors it finds. I have used the term *virulent*, because it is conceivable that an organism might remain alive in a soil long after losing all power to infect plants, just as we know it can in culture media. *Bacterium Solanacearum* causing brown rot of *Solanaceae*, *Bacillus phytophthorus* causing basal stem rot and tuber rot of the potato, and *Bacterium tumefaciens* causing crown-gall, certainly live in the soil, and the soundest plants when set in such soils, especially if wounded, are liable to contract the disease, if they belong to susceptible species. The root-nodule organism of *Leguminosae*, which I have not considered here, also lives in many soils, as every one knows.

MORPHOLOGY AND CULTURAL CHARACTERS OF THE PARASITES

Most of the plant bacteria are small or medium sized rod-shaped organisms. Very few parasitic coccus forms are known. In fact, none are very well established. Some of these bacteria are Gram positive, others are not. All take stains, especially the basic anilin dyes, but not all stain with the same dye or equally well. Most of the species are motile by means of flagella—polar or peritrichiate. A few are non-motile, genus *Aplanobacter*.¹ Some develop conspicuous capsules, others do not. Few, if any, produce endospores. Grown pure on culture media in mass, they are either yellow, pure white, or brownish or greenish from the liberation of pigments. Red or purple parasites are not known. We formerly supposed that there were no green fluorescent species capable of parasitism, but now several are known, e. g., the organism causing the lilac blight of Holland, with pure cultures of which the writer obtained typical infections at Amsterdam in 1906, and afterwards in the United States (now first recorded). Some species produce gas, liquefy gelatin, consume asparagin, destroy starch, and reduce nitrates; others do not. Their fondness for sugars and alcohols is quite variable. Some are extremely sensitive to sunlight and dry air (*Bacillus carotovorus*, *Bacillus tracheiphilus*). Others are remarkably resistant, remaining alive and infectious on dry seeds for a year (*Bacterium campestre*, *Bacterium Stewarti*, *Aplanobacter Rathayi*). Some are strictly aerobic, others can grow in the absence of air, if proper foods are available. Some are very sensitive to acids, alkalies and sodium chlorid, others are not. Some have wide ranges of growth from 0 C. upwards. Some will not grow at or near 0 C., others will grow at or above 40 C. Very few, however, will grow at blood temperature, certain ones even in plants or on culture media are killed by summer temperatures, and none are known definitely to be animal parasites.

¹ Smith, E. F. Bacteria in relation to plant diseases. Carnegie Inst. Washington. Publ. 27¹: p. 171. 1905; *Ibid.* 27²: pp. 155, 161. 1914.

ACTION OF THE PARASITE ON THE PLANT

In some cases it is hard to draw the line between parasitism and symbiosis or mutualism. Probably we shall find more and more of these transition states. I have included *Ardisia* in my list of genera and have excluded the genera of legumes subject only to root nodules. But a nodule on the root of a legume, so far as the local condition is concerned, is a disease as much as a leaf-spot, and, if Nobbe and Hiltner's statements are to be credited, the general effect of the root-nodule organism on the plant may be excessive and injurious and not to be distinguished from a disease.¹

In the tropical East Indian *Ardisia*, which is one of the strangest cases of mutualism known to me, and on which Miehé has done such a beautiful piece of work, we perhaps have something akin to what occurs in the root nodules of legumes. Here the bacterial injury is local and internal. There are no superficial indications of disease. The bacteria are most abundant in the leaf-teeth where they form pockets or cavities and multiply enough to make the leaf serratures appear blanched or yellowish and slightly swollen, but never enough to kill them. In smaller numbers the bacteria occur in other parts of the plant including the inner parts of the seed from which they are transmitted to the seedling, whose leaf serratures, infected through their water-pores, in turn become the chief focus of the bacterial multiplication. Apparently the bacteria are always present, and we do not know what would happen to *Ardisia* plants grown without them, nor do we know how to obtain such plants. It would be an interesting experiment to see if they could be produced and to watch their behavior.

The action of such organisms as I have mentioned differs probably from the behavior of active parasites in that they liberate much weaker toxins and enzymes, can attack only very actively growing parts, and also give off compensating nitrogenous substances. Not yet proved for *Ardisia*.

¹ Smith, E. F. Bacteria in relation to plant diseases. Carnegie Inst. Washington, Publ. 27²: p. 131, last paragraph. 1911.

The active parasites produce toxins freely, poisoning the tissues, and enzymes converting starches into sugars, complex sugars into simpler ones, and so on, for their nutrition. They also neutralize and consume plant acids, and feed upon amido bodies and other nitrogenous elements of the host. As a result of their growth, many of them liberate both acids and alkalis to the detriment of the plant. The solvent action of their products on the middle lamellae separates cells and leads to the production of cavities in the bark, pith, phloem and xylem. There is also, or may be, a mechanical splitting, tearing or crushing due to the enormous multiplication of the bacteria within confined spaces. The whole intercellular mechanism may be honeycombed and flooded in this way, and if the cavities are near the surface the tissues may be lifted up or the bacteria may be forced to the surface through stomata in the form of tiny beads or threads (pear, plum, bean, maize, sugar-cane, etc.), or by a splitting process. The splitting in the black spot of plum fruits and peach fruits, however, results from local death of the attacked tissue with continued growth of the surrounding uninjured parts.

A majority of the forms known to cause plant diseases are extra-cellular parasites occupying chiefly the vessels and intercellular spaces, causing vascular diseases, soft rots, spot diseases, etc. But intra-cellular parasites also occur, e. g., *Bacterium Leguminosarum* causing root-nodules on legumes, and *Bacterium tumefaciens* causing crown-gall. The former multiplies within the cell myriadfold, prevents its division, destroys its contents including the nucleus, and enormously stretches the cell wall so that the cell becomes much larger than its normal fellow cells and is packed full of the bacteria. The latter does not multiply abundantly within the cell, does not enlarge it, does not injure its viability, and would be a harmless messmate were it not for the fact that it exerts a stimulating effect on the cell nucleus, compelling the cell to divide again and again.

THE REACTION OF THE PLANT

We now come to the reaction of the plant. What response does it make to this rude invasion? Ten years ago we might

have said, "With rare exceptions, the plant is passive or nearly so," but that would have been a superficial observation.

In every disease we must suppose that the plant makes some effort to throw off the intruder, although often its forces are paralyzed and overcome very early in the progress of the disease.

One of the most conspicuous results is lessened growth. In some of my plants recovering from brown rot due to *Bacterium Solanacearum*,¹ a month after external signs of the disease had disappeared the check plants were twice the size of the inoculated ones, and there was still a very decided difference after more than two months. I do not know how to explain this checked growth unless it be the response to absorbed toxins.

On potato plants attacked early by *Bacterium Solanacearum* the tubers remain small. On maize attacked by *Bacterium Stewarti* the ears are imperfect. Olive shoots inoculated and infected by *Bacterium Savastanoi* are always dwarfed, and the crown-gall dwarfings are frequently very conspicuous. The dwarfing of melon and squash plants attacked by *Bacillus tracheiphilus* is also conspicuous. Uninoculated sugar-cane stems soon surpass in height and vigor those successfully inoculated with *Bacterium vascularum*.

Changes in color are also conspicuous. The attacked parts may become greener than normal, or fade to yellow, red, brown or black. In tomato fruits there is often a retarded ripening on the attacked side with persistence of the chlorophyll. Crown-galls on daisy are greenish. In certain leaf-spots also the leaf green persists in the vicinity of the spot while the rest of the leaf becomes yellow (bean-leaf spot). The male inflorescence of maize attacked by *Bacterium Stewarti* ripens prematurely and becomes white.

Distortions of various kinds appear (leaves of bean, lilac, larkspur, hyacinth, mulberry, Persian walnut). The leaves of tomato plants attacked by *Bacterium Solanacearum* are bent downwards; so are the fronds of the coconut palm when

¹ Smith, E. F. Bacteria in relation to plant diseases. Carnegie Inst. Washington, Publ. 27^s: pl. 45-D. 1914.

attacked by the bacterial bud-rot. Knee-shaped curvatures of the culms appear on *Dactylis* attacked by *Aplanobacter Rathayi*, and in the buds of the sugar-cane attacked by Cobb's disease.

Organs may be developed in excessive number or out of place, as roots in hairy-root of the apple, witch-brooms on *Pinus*, and incipient roots on the stems of tomato, tobacco, chrysanthemum, nasturtium, etc. Hunger found a bud on a tomato leaflet which he attributed to the stimulus of *Bacterium Solanacearum*.

In various diseases the plant removes starch from the vicinity of the bacterial focus which it endeavors to wall off by the formation of a cork barrier, and in this effort it is sometimes successful if the parasite is growing slowly.

The most conspicuous response of the plant is in the form of pathological overgrowths,—cankers, tubercles, and tumors. Some of these are very striking, e. g., those on the ash, olive, pine, oleander, and on a multitude of plants attacked by crown-gall. In some of these growths there is a great reduction of the vascular system, and a great multiplication and simplification of the parenchyma. There are also various other phenomena nearly related to what takes place in certain insect galls. In crown gall cell division under compulsion proceeds at such an abnormally rapid rate that the cells are forced to divide while still immature, and in this way masses of small-celled unripe (anaplastic) tissue arise. These develop tumor-strands on which secondary tumors arise.

PREVALENCE AND GEOGRAPHICAL DISTRIBUTION

Economically considered, bacterial diseases of plants may be classed as major or minor. Most of the leaf-spots would fall into the latter class. Various soft rots, blights and vascular diseases, being wide-spread and destructive to plants of great economic importance, may be classed as major diseases. Cankers and tumors would fall midway in such a grouping. Occasionally a minor disease, e. g., lettuce rot, celery rot, under favorable conditions may assume great importance.

It will be of interest to mention a few of these diseases with particular reference to their distribution and prevalence.

Dutch East Indies.—The tobacco disease of Sumatra and Java is probably the most destructive, if the Sereh of sugar-cane is not bacterial. Each of these diseases has caused enormous losses. Each threatens an industry. The tobacco disease occurs also in the West Indies, in the United States, and probably also in South Africa. If Janse's root disease of *Erythrina*, the coffee shade tree of Java, is also bacterial, as he supposed, then there is another great bacterial plague in that region, for hundreds of thousands of trees have died, and another species has been substituted as a shade tree.

West Indies.—Here the most destructive disease is the bacterial bud-rot of the coconut palm, which occurs all around the Caribbean, and threatens the entire destruction of a profitable industry in Cuba. There is also the bacterial disease of bananas and plantains, but the most wide-spread and destructive *Musa* disease of the Western Hemisphere is the Panama disease, due to a *Fusarium*.

Australia.—Cobb's disease of sugar-cane has probably attracted more attention in Australia than any other bacterial trouble, although bacterial rots of the potato are also very destructive. The cane disease in both Queensland and New South Wales has in many cases destroyed the output of whole plantations and greatly discouraged planters. This disease occurs also in Fiji, and probably in South America.

Japan.—Probably the tobacco wilt, which has destroyed many fields, is the worst Japanese disease. This is believed to be identical with the tobacco wilt of Sumatra and of the United States. Several other bacterial blights have been reported, including one of the basket willow.

India.—The brown rot of *Solanaceae* is common and destructive. Most of Asia is a *terra incognita*.

South Africa.—The mango disease in recent years has greatly reduced the exports. Potato and tomato wilts are common. There is a serious tobacco disease, probably bacterial. Crown-gall is common and injurious on shade and orchard trees. Other diseases occur.

South America.—There is a serious disease of sugar-cane in Brazil and another in Argentina, both of which I believe are of bacterial origin, and identical with Cobb's disease. Bondar has reported a destructive manihot disease. The bud-rot of the coconut occurs in the north.

United States and Canada.—Potato rots probably cause the greatest losses one year with another. Following these I should think pear and apple blight. Perhaps the latter should be placed first, for the destruction of an acre of potatoes would scarcely equal the value of a single fine pear tree, and thousands are destroyed every year. In California, which was free from pear blight until recently, the losses in the last fifteen years have been enormous, amounting to about one-third of all the full-grown orchards and to a money-loss estimated at \$10,000,000 for the five years preceding the efforts for its restriction begun in 1905 by the U. S. Department of Agriculture. Very serious losses from this disease are experienced every year in the East, or were until growers became generally familiar with methods of control.

In our southern states the tobacco and the tomato wilt have made it impossible to grow these crops on many fields. In the northern United States the cucurbit wilt is wide-spread and destructive, but cucurbits are of course a minor crop.

The walnut blight has done much damage in California. This occurs also in New Zealand and Tasmania.

The bacterial disease of alfalfa has been serious in parts of the West. It is most injurious early in the season, i. e., on the first cutting.

Holland.—Here the yellow disease of hyacinths is always destructive and will eventually put an end to hyacinth-growing for export if means cannot be had for its control, since the land suited for hyacinths is limited in amount. Brown rot of cabbage occurs in Holland and Denmark, and is common now also in many parts of the United States. It was probably imported into the United States from Denmark on cabbage seed. Some years in nurseries about Amsterdam the lilac blight has been troublesome.

Great Britain and Germany.—Potato rots are probably the most destructive bacterial diseases.

France and Italy.—Potato diseases are common. Olive tubercle, common also in California, and all around the Mediterranean, is prevalent in spots. Vine diseases, especially *Maladie d'Oleran* and crown-gall, do considerable damage. Pear blight seems to be absent in France, but has been reported from several places in Italy. The destructive Italian rice disease, *brusone*, is not due to bacteria as reported, but to a fungus (*Piricularia*).

METHODS OF CONTROL

In conclusion, some words on prophylaxis will be in order. Until recently almost nothing was known. Unfortunately so far as regards most of these diseases, methods of control must still be worked out. But with rapidly increasing knowledge of the biological peculiarities of the parasites causing these diseases, and of the ways in which they are disseminated, light begins to dawn, so that before many years have passed we may confidently expect the more intelligent part of the public to be applying sound rules for the control of these diseases,—rules based on the individual peculiarities of the parasites and carefully worked out experimentally by the plant pathologist.

The little that we now know may be summarized in part as follows:

Waite has shown that pear blight winters over in exceptional trees on trunk and limbs in the form of patches which ooze living bacteria the following spring and are visited by bees and other insects, and that if these “hold-over” spots are cut out thoroughly over regions several miles in diameter (wide as a bee flies), the disease does not appear on the blossoms and shoots the following spring, except as it is introduced into the margins of this area from remoter uncontrolled districts. He has tried this method of control very successfully, both in Georgia and California. Sometimes only one tree in many carries over the disease, but such is not always the case, and the success of this method involves the inspection of every pome tree in a district with complete eradication

of every case of the hold-over blight, and this in great fruit regions requires a small army of trained inspectors. During the blighting period in late spring and early summer, if one would save his orchard, the trees must be cut over for removal of diseased material as often as every week, and in the worst weather oftener.

The introduction of diseases transmitted by way of seeds, bulbs, and tubers may be avoided by obtaining these from plants not subject to the disease. As this freedom cannot always be known, bulbs and tubers should be inspected critically before planting, and firm-coated seeds should be soaked for 15 minutes in 1:1000 mercuric chlorid water. In case of two plants (cabbage and maize) we know positively that the diseases are transmitted on the seed and this is probably true for several others—beans, sorghum, orchard grass. All shrivelled seeds should be screened out before planting.

The seed bed in case of tobacco, tomato, cabbage, and transplanted plants generally, should be made on steam-heated or fire-heated soil, or new earth which one has good reason to think free from the parasite in question.

Nematode-infected soil should be avoided.

Cuttings of carnations, chrysanthemums, roses, peaches, plums, apples, quinces, sugar-cane, etc., used for slips, buds, or grafts should be from sound plants. By following this practice, recommended in case of sugar-cane by Cobb, the more intelligent cane planters in New South Wales have overcome the disease due to *Bacterium vascularum*.

On badly infested soils a careful long rotation should be practised and the low places should be drained.

Certain diseases may be held in check by germicidal sprays. Pierce reduced the number of infections in walnut blight fifty per cent by this method. Scott and Rorer combated leaf-spot of the peach in this way, the sprayed trees retaining their leaves, the unsprayed ones becoming defoliated. ——— in Italy has recommended it and used it successfully on olive trees following hail-storms to keep out the olive tubercle.

When diseases are transmitted by insects the destruction of the latter must receive prompt attention.

Great care should be taken to keep the manure heap free from infection. Diseased rubbish should be burned or buried deeply. It must not be thrown into a water supply or fed to stock or dumped into the barnyard.

It has been found that some varieties of plants are less subject to disease than others (pear, apple, plum, maize, potato, tomato, sugar-cane, banana, cabbage, etc.), and there are also individual variations within the variety. These phenomena lead us to hope that by selection, or hybridization, valuable resistant strains may be originated. Meanwhile the resistant sorts when they are of any value commercially should be substituted for sensitive sorts in localities much subject to the disease. Unfortunately some of the resistant sorts have other less desirable qualities. A vast amount of experimental work must be done in this field before we shall have substantial results, and at least a generation or two will be required to learn even the boundaries of the field. But the problem offered is so enticing and has such immediately practical bearings that in the near future we may suppose many pathologists will devote themselves to it, and that long before the whole field is worked over, many useful results will be forthcoming. The labor involved is enormous and exacting to discouragement at times, the results come so slowly, so much must be done to be certain of so little, all because the organisms dealt with are very small—*how small*, we seldom realize!

Many a time in the past when downcast I have repeated to myself Seneca's rolling words, *Palma non sine pulvere per viam rectam*, and have had more or less encouragement out of them. They are a good motto for any man, since nothing is more certain than this, that without plenty of well-directed hard work there can be no worthy success in any field of human endeavor.

